

The University of Chicago

ALPINE PLANT SUCCESSION ON JAMES
PEAK, COLORADO

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
CLARE FRANCIS COX

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
ECOLOGICAL MONOGRAPHS
Vol. III, No. 3, 1933

The University of Chicago

ALPINE PLANT SUCCESSION ON JAMES
PEAK, COLORADO

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
CLARE FRANCIS COX

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
ECOLOGICAL MONOGRAPHS
Vol. III, No. 3, 1933

CONTENTS

	PAGE
Introduction	301
Geologic History	302
Physiography	303
Climatic factors	304
Temperature	304
Light	307
Precipitation	308
Growing season	310
Exposure, altitude, slope	311
Wind	311
Evaporation	312
Humidity and soil moisture	316
Soil	316
Biotic factors	318
Grazing	318
Fire	319
Clearing	319
Vegetation	319
Introduction	319
Methods	321
Alpine scrub forest; tension zone communities	322
Alpine desert; pioneer communities	325
Boulder fields	326
Fell fields	328
Talus slides	330
Alpine grassland; alpine meadow communities	331
Scrub associations	332
Salix scrub	332
Dryas scrub	333
Snow flush associations	334
Alpine moor associations	336
Wet meadow associations	338
Mesophytic meadow associations	343
Dry meadow associations	347
Alpine meadow climax; Elynetum	350
Alpine succession	355
Alpine plants of James Peak	357
List of species	359
Discussion	367
Summary	370
Bibliography	371



ALPINE PLANT SUCCESSION ON JAMES PEAK, COLORADO¹

INTRODUCTION

Comparatively little has been done on this continent in the investigation of environmental conditions and plant succession in the alpine zone of the high mountains and in the arctic region. Data concerning conditions affecting plant life in these regions are extremely limited. The present work is the result of a fairly intensive study made of a small area in the alpine zone. In addition to methods commonly applied in the investigation of the vegetation by American ecologists, the writer has used the statistical method as employed by European investigators in their study of the plant associations in the Alps and in northern Europe.

The summers of 1928 and 1929 were devoted to the work in the field, practically the entire vegetative season being spent within the alpine zone. Limitations as to time and facilities available for carrying on field work in the mountains far above all settlements in a region where severe storms frequently interrupt the short growing season made it impossible to carry on detailed study of all the important factors. Quantitative measurements were made of altitude, exposure, temperature, length of growing season, evaporation, and soil acidity. General observations only were made of the effect upon the plants of the climatic factors, light, rainfall, wind, and soil. Attention was also directed towards the effect of the biotic factors, grazing, fires, and lumbering. The statistical method of Raunkiaer with certain modifications was used to determine the floristic composition of the plant associations and to trace the origin, development, and decline of these units of vegetation. Considerable attention was given to the presence in a given community of certain plant species of well defined life requirements as indicators of ecological conditions in the habitat. Such species may sometimes serve to a certain extent as a check on the data obtained by instruments or upon conclusions reached by a more or less superficial study of a habitat. A passive inorganic instrument does not always measure the effect of a particular stimulus upon living protoplasm.

Grateful acknowledgment is hereby made to Professor George D. Fuller of the Department of Botany, University of Chicago, for advice and criticism throughout the present study; to Aven Nelson, A. S. Hitchcock, C. R. Ball, C. C. Plitt, Theodore Holm, and Kenneth K. Mackenzie for their liberal and valued assistance in the determination of the plants; to my wife, Lissa, for help in the collection and preservation of the plants and for assistance in making the plant population studies upon which the work is so largely based; and

¹ A contribution from the Hull Botanical Laboratory, University of Chicago.

to Mr. and Mrs. Oliver W. Toll of Denver, Colorado, whose generous hospitality facilitated the carrying out of the investigation. The writer furthermore welcomes this opportunity to express his gratitude for the assistance afforded in carrying on this work by the John Merle Coulter Research Fellowship in Botany.

GEOLOGIC HISTORY

The area to which this study has mainly been confined comprises some ten or twelve square miles extending eastward from James and Parry Peaks, (Fig. 1) which lie along the crest of the Continental Divide, to the site of the

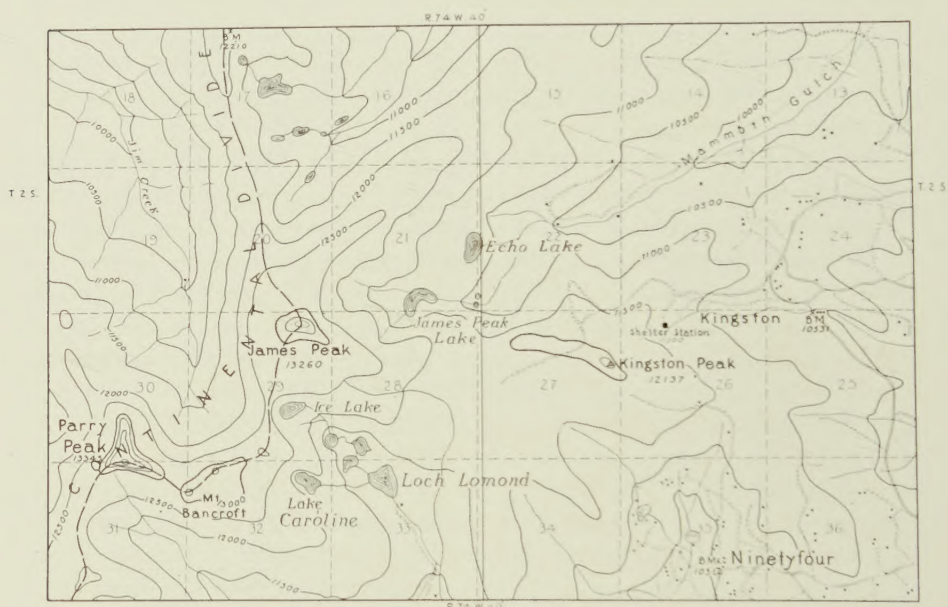


FIG. 1. Map of James Peak, Colorado. The area under investigation extends from James and Parry Peaks on the Continental Divide eastward to Kingston village. (U. S. Geol. Surv. Colo. Central City Quadrangle, modified by omission of all but 500-foot contours except on Kingston Peak above 12,000 feet and on James, Parry, and Bancroft Peaks above 13,000 feet where 100-foot contours are retained.)

former village of Kingston. James Peak is about forty miles almost straight west of Denver. The region lies within the area marked on geological maps of Colorado as Pre-Cambrian which is described by George (1927) as being a complex of granites, gneisses, and schists rendered extraordinarily complex by intrusions of granite and other igneous rocks. Sedimentary deposits of Pre-Cambrian or later eras, as well as these igneous intrusions, have either been removed by erosion or have been so completely metamorphosed as to have lost their original structure. Limestone does not occur within the area.

The scanty soil which sometimes overspreads the gentler slopes and valleys or is lodged among the rocks has resulted from the weathering of the

crystalline rocks and from the decay of plant remains. Much of the area is a broad upland, a large part of it possessing a comparatively gentle relief for mountain territory of such great elevation, and showing little or no sign of glacial action. But two great cirques, one at the head of Mammoth Gulch to the northeast of James Peak, containing Echo and James Peak Lakes, and one to the south, containing Loch Lomond and Ice Lake (Fig. 2), constitute evidence of ice erosion during Pleistocene times. All these lakes owe their existence to the work of mountain glaciers, the heads of which were at the upper end of the valleys some distance above timberline. The uplifting of this region to its present elevation took place mainly in the late Tertiary Period (Blackwelder and Barrows 1911), and subsequent erosion is responsible for the present relief. The altitude varies between 10,500 and 13,345 feet, but the greater part of the vegetation dealt with in the present study occurs on the mountain slopes between 11,000 and 13,000 feet.

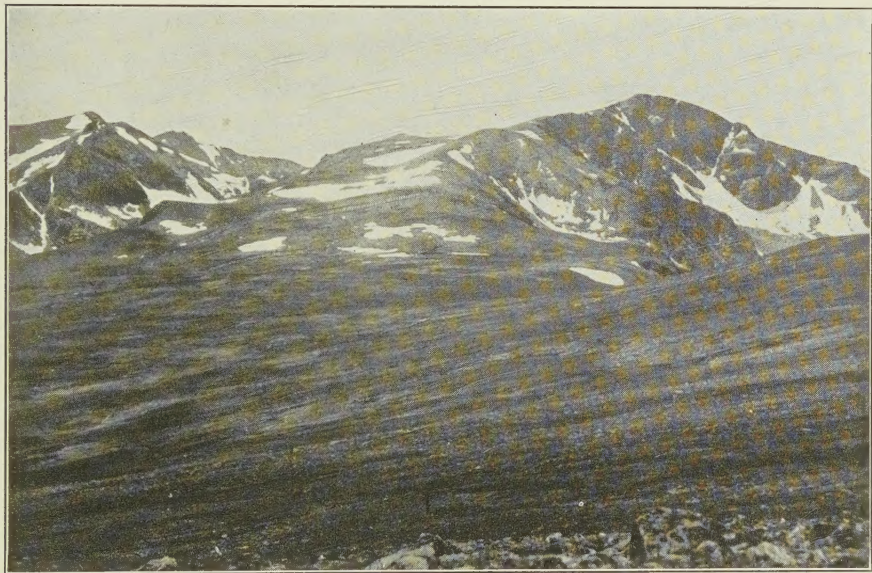


FIG. 2. Alpine expanse looking southwestward from Kingston Peak towards Continental Divide. James Peak and glacial cirque at head of Mammoth Gulch at right; Parry Peak in left center and Mt. Bancroft at extreme left. Large gulch between James Peak and Mt. Bancroft heading against Continental Divide. Photographed July 1, 1931.

PHYSIOGRAPHY

Outstanding in alpine altitudes, at least until later stages of the erosion cycle are reached, is the barrenness resulting from the great amount of exposed rock. Due to vigorous action of wind, water, and ice, soil is not permitted to accumulate over much of the region even though soil forming forces may be active. Great boulder fields commonly occur on top of massive

summits such as are characteristic of James and many other peaks of the Colorado Rockies. Boulder fields are also frequently encountered on rounded ridges, on mountain flanks of moderate relief, and at the foot of precipitous slopes and cliffs. Slides or talus slopes of unstable rock fragments extend upward from the bases of steep slopes and precipices. In cracks and crevices of the rocks and on flat ledges and surfaces of moderate relief the smaller particles of rocks waste are first permitted to accumulate, and it is in such places that the first vascular plants gain foothold. Since there are many species of plants that can withstand the rigors of the alpine climate on James Peak, the great barrenness of much of the region is due to activity of erosion, to lack of soil, and to late lying snow which in many places reduces the growing season too much to permit plants to complete their life cycle.

Two deep gulches were carved out of the rock by the Pleistocene ice. The upper ends of these glacial valleys for a short distance lie within the area under investigation. Sufficient time has not elapsed since these valley floors were swept clean by the ice for the present streams to entrench themselves in the hard rock. Only a comparatively thin covering of soil has been formed and in many places it is coarse in texture and contains little humus. The greatest soil-accumulations occur in marshy areas about streams and lake margins and at the foot of many of the slopes around the valley, especially at the lower edge of snow drifts in places favorable for the development of vegetation.

Upon the upper mountain slopes in places of moderate relief, the mantle rock has perhaps been less disturbed for a much longer period except on surfaces exposed to wind. Few of the streams on these slopes are of any size, and only three or four of them flow continuously throughout the season. During early summer while the snow is melting and during late summer for a few hours following heavy showers, they are active carrying rock waste down the slopes; but due to the hardness of the underlying rock they have nowhere cut any deep channels. Here, as in the glaciated valleys below, the most extensive soil deposits occur about springs and seepage areas and along stream-sides where soil formation is favored.

CLIMATIC FACTORS

Temperature.—The limited data available concerning winter temperatures in the higher Rockies come from records kept for a few years on Pike's Peak, at Corona, which is on the Continental Divide a few miles north of James Peak at 11,660 feet, and from occasional reports from isolated points in the mountains. The records kept at Corona (Dodds 1917) indicate a mean annual temperature of 26°F. for that altitude and show that frosts may occur almost any week during the summer. The 26° isotherm on a temperature map of the world passes through Alaska, Labrador, and Greenland. This indicates for the high alpine region a climate approaching closely

that of the arctic. However, it seems certain that much lower temperatures are reached in Montana and various parts of Canada at moderate altitudes where forests are well developed than in the alpine regions of Colorado. Studies made in the Alps (Brockmann-Jerosch 1919) on the relation of low temperature to the occurrence of tree vegetation indicate that length of growing season and exposure to desiccating effect of winds during periods when the ground is frozen are more critical than winter temperatures in determining the tree limit in the alpine zone and in the far North.

The thin atmosphere at these high altitudes has little capacity for retaining heat and it changes temperature rapidly after the sun disappears. Heat is quickly radiated from rocks and soil at night. A wide range in daily temperature is noticeable during the summer months. Low temperatures during the alpine growing season are decisive in their effect on the vegetation. Late frosts may destroy new growth in late spring or summer; and where the growing season is so brief, it will not permit a second growth to reach maturity. Great contrasts occur between sun and shade temperatures and between south and north exposures. This is very noticeable in the difference in time of flowering of species occurring in both locations.

During the summers of 1928 and 1929 complete records were kept of daily maximum and minimum temperatures at a station at the lower edge of the alpine zone at 11,300 feet (Table I). The thermometers were placed on the northwest side of a building where they were sheltered from the direct rays of the sun at a height of four feet above the ground. The record maintained at this station from June 28 to August 27, 1928 and from June 21 to August 26, 1929 covers practically the entire growing period in the alpine zone and shows temperatures of 32° F. or lower in 1928 on June 28, July 1, 8, 25, August 3, 4, 23, 24, 26, and 27. The record for this same period during 1929 kept at the same station with the same thermometers failed to show a single freezing temperature although the record for this second summer shows temperatures of 40° or lower on 22 different days. The maximum temperatures were practically the same during 1928 and 1929, averaging 65° both summers and reaching 70° or above, 15 times in the former year and 13 times in the latter. The minimum temperatures averaged 39° in 1928 and 41° in 1929. The mean daily temperature for these two seasons is therefore seen to be practically the same in spite of a considerable number of days with greater extremes in the summer of 1928.

The explanation of the differences in the two summers is relatively simple when one knows all the weather conditions during the two seasons. The summer of 1928 was, with the exception of a three week period, a dry summer with much bright sunny weather and relatively few cloudy, rainy days. The summer of 1929, on the other hand, with the exception of about three weeks, was almost continuously wet with most of the days cloudy or rainy. The cloudy condition and humid atmosphere in 1929 served to equalize the ex-

TABLE I—Daily summer temperature record

Date	1928		1929		Date	1928 (Cont.)		1929 (Cont.)	
	Max.	Min.	Max.	Min.		Max.	Min.	Max.	Min.
June					July (Cont.)				
21	..	..	66	36	25	58	32	70	42
22	..	..	64	35	26	66	40	74	45
23	..	..	58	40	27	60	42	64	45
24	..	..	58	34	28	64	39	59	35
25	..	..	64	35	29	66	40	62	43
26	..	..	65	46	30	64	46	63	42
27	..	..	70	42	31	70	45	60	43
28	64	32	74	40	August				
29	72	36	72	42	1	64	47	62	46
30	66	33	68	44	2	60	40	66	46
July					3	57	32	56	44
1	70	32	67	37	4	56	32	62	44
2	68	33	68	35	5	59	37	58	45
3	70	42	65	38	6	62	34	53	40
4	72	41	66	40	7	61	39	62	36
5	64	44	70	35	8	68	34	62	40
6	70	44	68	39	9	70	37	58	36
7	64	36	65	40	10	66	38	60	40
8	66	31	70	36	11	68	40	64	40
9	72	42	65	38	12	68	45	64	36
10	78	38	65	40	13	67	42	66	35
11	74	38	66	39	14	70	42	68	40
12	72	37	67	43	15	63	44	70	46
13	70	40	68	39	16	61	42	73	47
14	66	44	67	43	17	67	36	66	43
15	68	38	72	38	18	70	46	64	38
16	66	45	76	44	19	64	36	66	44
17	59	40	70	44	20	65	46	65	42
18	68	42	66	40	21	70	42	62	45
19	64	42	69	43	22	66	48	64	41
20	65	42	66	47	23	53	28	62	38
21	62	40	69	43	24	60	29	64	43
22	63	39	70	42	25	56	42	60	42
23	56	38	65	45	26	54	30	64	42
24	53	36	64	41	27	56	27	..	..

	1928	1929
Mean Daily Temperature.....	52	53
Mean Maximum Temperature.....	65	65
Mean Minimum Temperature.....	39	41
Mean Daily Temperature Variation.....	26	24

treme temperatures of bright warm days and clear frosty nights such as occurred in 1928.

Soil temperatures at the surface of the ground may be considerably different from air temperatures four feet above the ground. Differences in sun and shade temperatures are considerable at the same distance above the surface. A few soil temperatures taken at the surface of the ground on a south sunny exposure at the station showed a temperature as high as 90° at 11:00 A. M., when the thermometer in the station registered 70°. Ice was formed on a small mountain rill near by on nights when the thermometer at the station registered no lower than 37°. A daily temperature range of

40° F. was obtained there; but the ranges at the soil surface at this altitude were noticed in a few instances to be as great as 60° F. in a 24 hour period. Consequently, the temperature record as kept gives only a limited idea as to the extremes which occur in the alpine zone.

The significance of the temperature factor in its effect upon alpine vegetation can best be appreciated when one considers the low daily minimum and the frequency with which the temperature reaches or approximates the freezing point during the brief growing season. The maximum temperature often comes between 10:00 and 11:00 A. M. Frequently the wind arises or clouds form about this time, and the temperature soon falls. On very few days does high temperature last long. It is always cool by sunset and remains cold all night. Such conditions must be effective in dwarfing and in otherwise determining the characteristics of the plants of the region.

The data collected are sufficient to show that in much of the alpine zone at least freezing temperatures may be reached at any week during the growing season. The alpine growing season then cannot be measured in frostless days as is frequently the practice in lower altitudes. The vegetation must consist of plants which can survive in spite of these extreme temperatures. Along the bottoms of valleys, especially in deep canyons, cold air may flow down for considerable distances, the late freezes destroying species which are able to survive on the higher slopes. Late lying snows may accumulate in such places and prevent the plants of lower altitudes from occupying them. Alpine species frequently occur in such places at lower altitudes than on the higher valley sides where subalpine vegetation may prevail. Tree vegetation is frequently absent from the valley floors while alpine meadows border the streams and extend down into what appears, from the forests on the valley slopes, to be subalpine zone. Alpine growing conditions may thus be extended to lower altitudes.

Light.—Light varies more perhaps in different parts of the alpine zone than at lower altitudes. This is made possible because of the high altitude, the thin transparent atmosphere, and the areas of snow with high reflective capacity. A large proportion of the light received by alpine vegetation is direct, and a smaller proportion is diffuse than is the case with vegetation of lowlands. Frequent cloudiness, however, reduces the total light received and converts a large proportion of direct to diffuse light.

Several theories have been advanced concerning the effect of the intense light upon the plants. Intense light is known to be destructive to chlorophyll. Henrici (1918-19) found that leaves of alpine species contain less chlorophyll than the same species from lower zones. Schanz (1918, 1918, 1919) thinks the ultra-violet light waves are responsible for the dwarfed condition of the plants, the brilliant colors of the flowers, and the thicker leaves with increased palisade tissue and lignification.

Since different species have different light requirements, the matter of

distribution into communities is influenced by the light factor. Plants growing on steep north slopes, in deep narrow valleys, in the shadows of boulders, and in lower layers of several-layered communities, such as the wind timber, commonly have thinner leaves with more chlorophyll than do plants growing in open meadows or other places exposed to the sun; e. g.: *Viola biflora*, *Saxifraga caespitosa*, *Adoxa moschatellina*. Species of extremely low light requirements, such as certain lichens, mosses, and flowering plants which may come almost into flower before the snow is completely removed, are frequently to be found where snow lies until late summer. Plants with leaves covered with hairs or sometimes with scales are characteristic of exposed situations; e.g.: *Eritrichium argenteum*, *Actinea lanata*, *Trifolium dasyphyllum*, *Artemisia pattersoni*. Plants of exposed habitats are pronouncedly xeromorphic. Those subject to the desiccating action of both sun and wind are most decidedly so. Fell fields on southwest exposures are sometimes almost devoid of vegetation except in cracks and crevices which afford shelter against sun and wind.

Precipitation.—The major portion of the precipitation in the alpine zone is in the form of snow and occurs while vegetation is inactive. The rain comes commonly during the summer months in showers of brief duration occurring about noon. Data concerning the annual precipitation in alpine altitudes in the Rockies are extremely limited. The weather station maintained for several years on the Continental Divide a few miles north of James Peak recorded a total precipitation of 43.69 inches (Dodds 1917). The snowfall amounted to 390.6 inches (32.5 feet). Snows may occur during any month but come mostly from September to May. The rain occurs in June, July, and August. Sleet and hail are not infrequent during July and August. Records kept on Pike's Peak (Whitfield 1933) at montane, sub-alpine, low alpine, and high alpine stations show a gradually increasing precipitation with increasing altitude up to the lower alpine zone and a decreased precipitation above. This is in accord with records kept in the Alps.

In the present investigation the data concerning rainfall are limited to rather detailed daily observations concerning showers, state of the atmosphere with reference to clouds, mists, and wind. In case of rain, the time, duration, and intensity of the precipitation were noted. Such a record made it possible afterwards, when interpreting the quantitative data obtained in the evaporation studies, to determine the kind of weather at any time during the summer.

Table II summarizes some of the observations on precipitation, humidity, wind and light factors during the course of the investigation recorded in number of days. Under such a relative scheme it is, of course, difficult or impossible to classify some of the days; hence the totals in some cases may fail to account for the full number of days. The value afforded by such a scheme can best be appreciated when it comes to interpreting fluctuations

TABLE II—General observations on rainfall, wind, and humidity

	1928 June 24—August 27	1929 June 21—August 26
Length of period.....	65 days	67 days
Rain, heavy or prolonged.....	14 " }	26 " }
Rain, light.....	6 " }20	18 " }44
Rainless.....	43 "	23 "
Wind, brisk to strong.....	33 "	18 "
Wind, moderate.....	28 "	31 "
Calm (little or no wind).....	4 "	15 "
Bright, sunny most of day.....	32 "	12 "
Cloudy, much of day.....	17 "	49 "

in evaporation rates with respect to the possible part played by humidity, light, and wind in this process.

A study of the complete data kept indicates that in 1928 clear weather with moderate to brisk winds almost daily and only two or three light showers prevailed from June 24 to July 15. Then followed three weeks, July 15 to August 7, during which there were on an average two or three heavy showers each week and one or two light ones. There were only two or three bright days without rain each week. From August 7 to 27 the weather was fair again with only four heavy showers during the three weeks. In contrast with the 1928 season, that of 1929 started with a clear rainless period which lasted from June 20 to June 30. The stormy period then set in, lasting until August 6 with only about two rainless days each week and some weeks none. Storms frequently began by 10:30 to 11:30 and lasted late into the day, and occasionally into the night. August 7 to 15 was a period of bright, sunny, rainless days. The rest of the season, from August 15 to 26, was characterized by stormy weather with almost daily showers which were frequently of long duration.

The precipitation occurring during winter in the form of snow is of great importance to alpine vegetation. Snow acts as a reservoir for a considerable part of the water used by the plants during the growing season. Melting occurs so late and so gradually that the percentage of loss from run-off is less than would occur in case of the same amount of precipitation on the mountain slopes in the form of rain.

During bright rainless periods of early summer, water from melting snow maintains favorable growing conditions on many slopes. In years of little winter snowfall such periods are sometimes critical for certain species. In the Alps and in the Canadian Rockies a large perpetual snow cap furnishes water and more favorable conditions of humidity for the vegetation all summer.

While snow fields tending to assume the conditions of small glaciers are found on some of the higher peaks of northern Colorado, there is nothing

more extensive than large snowdrifts on James Peak. In sheltered places some of these frequently last throughout the summer. The size of the drifts and the time of their disappearance from most of the upland slopes vary considerably from year to year, indicating a considerable difference in the amount of snow in different years. In 1928 on July 12 there was considerable snow at elevations from 11,000 to 12,000 feet even on slopes exposed to the sun. In 1929 by July 1 most of the snow had disappeared. In sheltered places among the trees in the subalpine zone snow may frequently be found after it has disappeared from most of the alpine slopes.

Snow in the alpine region is of great importance aside from its value as a source of water supply. The whole matter of distribution of species and communities is intimately connected with the presence or absence of a winter snow-cover and with the time at which the snow disappears in summer. Due to the constancy of direction of the prevailing winds, the snow accumulates in the same places year after year and is blown off others leaving them exposed. Certain species, as *Erigeron melanocephalus*, require the protection of this cover; some, like *Arenaria sajanensis*, appear to be indifferent to it; still others, like *Trifolium nanum*, occur only on areas kept practically free from snow or in places from which snow disappears at an early date. The peculiar habit of growth of the wind timber is caused in part by its winter snow cover which weighs the trees down. The depth of the snow determines their height. Species like *Sibbaldia procumbens* and *Erigeron melanocephalus*, requiring snow protection and consequently associated in spots where snow lies late, give rise to the well known snow flush communities. Oswald Heer (1836) first called attention to such spots, applying the classic name "Schneetälchen" (snowflush). Some species characteristic of wind-swept fell fields are rarely found where snow accumulates and are sometimes referred to as snow avoiding plants. Zonation of the vegetation is frequently brought about by variations from no snow cover to deep covering of late-lying snow.

During 1928 there was considerable evidence that vegetation suffered during the periods of bright rainless days and brisk winds. Particularly on rocky slopes, with little soil, exposed to both wind and sun, certain species of plants in places where soil water was insufficient to replace the rapid transpiration loss appeared to dry up without maturing seed.

Growing season.—Alpine growing season varies with latitude, altitude, exposure, and duration of snow cover. The growing season for areas kept free from snow is best considered as the period during which most of the frost is out of the ground. For areas where snow accumulates, it is the number of days without snow cover. Data submitted in the discussion of temperature and snow fix this period as varying from about three and one one half months in the most favorable spots to a few days or no period at

all where snowdrifts last all summer. For most of the region it amounts to from six to ten weeks.

Since frost may occur during almost any week of the summer, alpine vegetation is limited to species able to withstand freezing temperatures during their vegetative activity, to complete the life cycle from bud to seed in a few weeks, and to persist by vegetative propagation during years when seed fails to mature. The brief growing season excludes annuals and ranks first among factors determining the species which can succeed in the alpine zone.

Exposure, altitude, and slope.—Exposure and slope are important in relation to light, wind, temperature, evaporation, and soil moisture in any region of noticeable relief. Differences in altitude can be neglected except on mountains. In high mountains the effect of great relief upon most climatic factors appears to be to intensify them somewhat in proportion to the relief of the region. This explains the wide variations in amount of soil and snow accumulations, in time of melting of snow, in time of blooming of a given species, and in the species and plant associations at stations in close proximity in the alpine zone. Habitats, species, and associations embraced in a few square miles may be as varied as in a lowland region extending over many degrees of latitude and longitude. The great diversity results from the wide range of intensities of the climatic factors made possible by extreme differences of exposure, altitude, and slope.

An aneroid barometer and a pocket compass were always carried for determining altitude and exposure. The slope was estimated as nearly as possible without special equipment. Data obtained are recorded and their significance is discussed in the sections dealing with the various climatic factors.

Wind.—Wind affects vegetation mechanically by its pressure and physiologically by increasing evaporation. The former action brings about transportation of pollen and seeds and causes deformation of the plant as a result of injury to growing points. The abrasive action of sand and snow and the distribution of snow and soil also represent this type of wind action. Constancy of direction of prevailing winds causes accumulation of snow in certain places year after year and exposure of others. Flat tops of patches of wind timber indicate the average depth of winter snow. Clumps of dead wind timber point to insufficient snow cover, possibly in combination with late freezing. The killing of branches or trees, in so far as it results from the desiccating action of the wind in increasing transpiration, illustrates the physiological effect of the wind upon vegetation. Spaces free from limbs on tree trunks just above snow level indicate that abrasive action is greatest at the surface over which the wind blows.

In windswept areas where vegetation has succeeded in developing a continuous sod, the surface may become broken in certain spots, and the strong wind may gradually extend the openings until basin-like depressions are laid

bare. (Fig. 10). In such places vegetation can regain foothold with great difficulty and only after a long period.

The upper limit of tree growth on mountains has been found to be determined not so much by low temperature as by the physiological effect of wind in increasing transpiration. Other contributing causes are not to be overlooked. The subject of alpine timberlines has been discussed in detail by Shaw (1909) and by Brockmann-Jerosch (1919) who give extensive bibliographies dealing with this topic.

Species possessing great resistance to wind injury characterize the vegetation of wind exposed areas of the alpine zone. Cushion and mat forms and the rosette habit so common on fell and boulder fields are types of growth adjusted to steady and long continued action of the wind such as occurs at high altitudes (Fig. 4). Certain plant associations are characteristic of wind swept ridges and mountain slopes. Extensive study has been made of this type of vegetation in Lapland by Fries (1913). On James Peak various lichens, *Trifolium nanum*, *Paronychia pulvinata*, *Arenaria sajanensis*, *Phlox caespitosa*, and *Dryas octopetala* frequently dominate plant communities in the wind-swept areas.

Zonation of the vegetation is conspicuous and definite where different degrees of exposure to wind are encountered in places in close proximity as on windward and leeward sides of a mountain ridge or of large boulders. Very different vegetation types occupy windward and leeward slopes. Cold air drainage in lower alpine altitudes frequently extends alpine conditions and vegetation lower along deep ravines and valley floors than on their sides.

In the present study only such information concerning wind velocity was secured as could be obtained from general daily observations, from the apparent wind effects on the vegetation in different exposures and altitudes, from the positions and amounts of snow accumulations, from evidences of wind erosion and deposition on different slopes, and from comparative rates of evaporation in different altitudes and exposures. General daily observations concerning wind are summarized in Table II.

Evaporation.—Evaporation is not an exact measure of the loss of water from plants. Devices for measuring evaporation can not take into account the modified rate resulting from stomatal control, from differences in density of cell sap in different species, or from possible changes in the permeability of plant membranes. Since the evaporation rate gives valuable information concerning transpiration and water relations of the plant, especially when considered in connection with precipitation, it is commonly determined as a means of gaining knowledge concerning the water economy of the plant community. Factors commonly recognized as affecting the evaporation rate are wind, temperature, humidity, and radiant energy.

Atmometers were operated in pairs at a number of stations at different altitudes and exposures in alpine and subalpine zones during the summers

of 1928 and 1929. Livingston porous spherical atmometers were used; the methods employed were those which have come to be practically standard for these instruments. More time was devoted to evaporation study in 1928 than in 1929. The object in 1928 was to get information concerning the relation between evaporation rates at different altitudes and at stations of different degrees of exposure to wind and sun. During 1929 the object was, in addition to making a comparison of evaporation rates during the two seasons at some of these same stations, to determine any differences which might exist in evaporation rates of places with plant populations showing different floristic composition; that is, rates in different plant associations irrespective of differences of altitude and exposure.

Strong contrast in the weather of the two summers was indicated by data on rainfall, light, wind, and temperature. This was emphasized by differences in evaporation data which show the integrated effect of these factors upon evaporation rate.

A study of Table III which summarizes the average daily evaporation

TABLE III—Average daily evaporation rates at alpine and subalpine stations

Stations	Slope	Exp.	Altitude	Daily evaporation rate in cc.	
				1928	1929
Sedge-grass meadow.....	10°	NW	10,500 ft. subalpine	32.6 Aug. 1-26	
Spruce-fir forest.....	8°	E	10,700 ft. subalpine	13.2 July 9-Aug. 26	
Wind timber (sheltered)....	8°	E	11,250 ft. transition	13.7 July 9-Aug. 26	7.0 July 12 - Aug. 26
Mesophytic meadow.....	10°	E	11,300 ft. alpine	31.0 July 9-Aug. 24	20.0 July 12 - Aug. 26
Dryas slope (exposed).....	15°	E	11,300 ft. alpine		24.0 July 12 - Aug. 26
Wet meadow.....	5°	E	11,500 ft. alpine		17.0 July 12 - Aug. 26
Dry meadow (exposed).....	15°	SE	11,500 ft. alpine	36.7 July 10-Aug. 26	24.3 July 12 - Aug. 25
Climax meadow: Elynetum.	15°	NW	11,500 ft. alpine		23.3 July 14 - Aug. 25
Fell field (exposed).....	20°	NW	11,900 ft. alpine	43.2 July 15-Aug. 26	24.5 July 12 - Aug. 25
Fell field (exposed).....	20°	SW	12,000 ft. alpine	46.5 July 10-Aug. 26	
Boulder field meadow transition.....	20°	NW	13,200 ft. alpine	23.8 July 15-Aug. 14	

rates for the two seasons at the different stations shows the highest rate on rather barren fell fields of the lower alpine zone, next highest on the open grassland of alpine meadow, and a very much lower rate in the forest vegetation of the subalpine zone below.

In general, the results obtained point to an increase in evaporation rate with increase in altitude and in degree of exposure to wind and sun to about mid-alpine altitude. Since but one station was maintained at high alpine and this for only thirty days, the evidence is probably insufficient to justify the conclusion that evaporation rates are less here, although the results obtained during the time this station was operated indicate such a relation. Since rainfall has been found to be less at high alpine levels (Whitfield 1933),

TABLE IV—*Comparison of daily evaporation rates at different stations during the rainy week of July 24-31, 1928 and the dry week of August 17-24, 1928*

Station	Slope	Exposure	Altitude	Daily evaporation rate	
				July 24-31	August 17-24
Spruce fir forest.....	8°	E	10,700 ft. subalpine	9.0 cc	18.6 cc
Wind timber (sheltered)...	8°	E	11,250 ft. transition	4.8 cc	17.1 cc
Dry meadow (exposed)...	15°	E	11,500 ft. alpine	21.9 cc	52.9 cc
Fell field (exposed).....	20°	NW	11,900 ft. alpine	27.3 cc	54.0 cc
Fell field (exposed).....	20°	SW	12,000 ft. alpine	26.8 cc	58.3 cc
Mesophytic meadow.....	10°	SE	11,300 ft. alpine	15.0 cc	44.6 cc

one is tempted to conclude that the condition responsible for the decrease in precipitation, which is probably lower vapor holding power of the air at this altitude, would result in a lower evaporation rate here than at somewhat lower elevations. Frequent clouds or mists about high mountain peaks when it is clear below suggest that the air is often more nearly saturated at this high altitude than at lower altitudes. At this high alpine station near the summit of James Peak at 13,200 feet on a northwest exposure, a mesophytic meadow appeared to be developing. This points to high humidity or to high soil-water relation. The latter might result from decreased evaporation. Exposure to sun was slight at this station, but no more so than at a station maintained at 11,900 feet which showed a much higher evaporation rate. Possibly the evaporation rate at the higher alpine station would have been greater had the station been operated throughout the month of August. As might be expected, stations located in the same vegetation type, e.g. wet and

dry meadows, but in positions of different exposure show considerable difference in evaporation rates even at the same altitude. Floristic composition varies as much at these points as does evaporation rate.

Table IV shows the daily evaporation for a week of rather consistently cloudy, rainy weather from July 24 to 31, 1928 and for a week of as consistently clear, windy, rainless days from August 17 to 24 during the same summer. The limited data available for the higher altitudes of the Colorado Rockies indicates that weather of such a character is typical of the alpine summer. Late July or early August frequently constitutes a wet season of from one to three weeks being preceded and succeeded by periods of clear weather with little precipitation. A comparison of the average daily evaporation rate for July 24 to 31, 1928 with the daily rate for the whole observed season of 1929 at three stations operated at identical points during the two summers and a similar comparison of the evaporation at these stations for August 17 to 24 with the rates for the whole season of 1928 is impressive. These comparisons show a rather convincing correlation between the inte-

TABLE V—Average daily evaporation rate of different vegetation types

Vegetation type	Locality	Investigators	Evaporation in cc.
Beech-maple forest.....	Indiana	Fuller (1914).....	7.0
Beech-maple forest.....	Indiana	Cain and Friesner (1929)	6.6
Pine dune forest.....	Indiana	Fuller (1914).....	10.4
Western climax forest.....	Washington	Weaver (1914).....	8.4
Alpine scrub forest.....	Colorado	Cox.....	10.0
Edaphic prairie grassland.....	Illinois	Fuller (1914).....	12.5
Western prairie grassland.....	Nebraska	Weaver (1914).....	20-30
Alpine mesophytic grassland.....	Colorado	Cox.....	25.5
Alpine climax grassland.....	Colorado	Cox.....	30.5
Alpine fell field desert.....	Colorado	Cox.....	43.2

grated action of wind, sunlight, and humidity and the rate at which evaporation proceeds. Data obtained from the other stations during these two particular weeks and during the entire season of either 1928 or 1929 are also consistent in indicating such a relation.

A comparison of evaporation rates in alpine plant communities with rates in lowland communities should throw some light on the differences of the vegetation of the regions. Table V gives results obtained by investigations in several communities in different regions.

While Table V gives merely average evaporation rates in the various vegetation types and not the extremes which doubtless are decisive in the case of evaporation as for other factors, it seems to point to a general trend towards increased xerophytism expressed in the vegetation of a region as one goes from a region of lower to one of higher evaporation rate. As previously mentioned, it is when studied in connection with precipitation and soil

moisture that evaporation can be considered as giving most valuable information concerning the water economy of a plant or a plant community.

Most significant in determining the vegetation of any region are not the average but the extreme conditions which may happen only occasionally. It is at such times that evaporation may become the limiting factor which determines the species able to survive in the alpine zone. Weaver and Himmel (1931) find that it is dry periods when soil water is low and evaporation rate high that are critical for vegetation. Winds by their desiccating action then produce serious injury to plants. A careful study of the climatic factors effective during the summer of 1928 with its frequent summer frosts, its wide daily temperature variations, and its periods of bright, windy, rainless days sheds more light on alpine vegetation in regard to the structure and general habits of growth of its individuals, in regard to the floristic composition of its plant associations, and in regard to the successional relationships existing between its plant communities than does a study of the relatively much more equable climate of the growing season of 1929.

Humidity and soil moisture.—Quantitative work in determination of humidity and soil moisture was not attempted. Only such information was obtained as could be inferred from observation of wind, light, clouds (mists), rate of drying of various objects, and the loss of weight of soils upon drying. The occurrence in a community of one or more species of which the soil water requirements have been pretty well established (Ramaley 1917, 1919) was regarded as giving fairly definite information concerning the water relations in the habitat. Rapid drying of wet vegetation, soil, and other objects following a shower indicates rapid changes in humidity in alpine altitudes.

The humidity factor is important because of its relation to loss of water through transpiration. Weaver and Himmel (1931) in their prairie studies find that soil moisture and humidity are most important factors in determining the species which can succeed. Total precipitation and average humidity are comparatively high in the alpine zone. Ordinarily showers are fairly frequent during the summer, and conditions of humidity and soil water, except for short periods, probably remain within the limits necessary for most of the plants of the region in spite of sudden and frequent fluctuations in humidity and rainfall. It is doubtless during rainless periods, such as occurred in the summer of 1928, accompanied by strong wind, low humidity, and high evaporation rate that soil moisture becomes deficient in exposed situations to a point critical for vegetation.

Soil.—Lack of stability, except on surfaces of moderate relief, prevents the development of alpine soils to anything approaching a state of maturity. Chemical processes are greatly retarded by the slight solubility of the silicate rock. The conversion of large rocks to smaller fragments is accomplished largely by freezing and by differential expansion of the contained minerals.

Activity of both wind and water tends to prevent the accumulation of the finer particles.

In cracks and between boulders soil accumulation may occur much sooner than upon fell fields or slides. In shallow basins, about seepage spots, and along low margins of streams and lakes vegetation and soil develop most rapidly. In such places and on less exposed slopes of moderate relief the vegetation in time almost completely stabilizes the surface. Certain species in each particular habitat act as humus formers so that the organic content of the soil tends to increase in all places which support any form of plant life. With addition of humus soil texture becomes finer. Upon moderate slopes, where soil forming activities have proceeded for long periods with little disturbance, the most mature soils of the region eventually develop.

Since only silicate rocks occur, it will be readily understood why only acid soil reactions obtain. Due to lack of basic materials, such as lime carbonate, the acid condition which develops from decomposition of complex silicates of crystalline rocks and from the growth of plants, is not neutralized. This acidity in combination with low temperature, poor soil aeration, and absence of soil organisms which cause decay promotes accumulation of a peatlike humus poor in plant nutrients. All the soil and even the water may show a distinctly acid reaction. Soils which develop in this manner are characteristic of the alpine zone in all regions lacking calcium carbonate. Humus content varies greatly from rock waste entirely destitute of organic material to moor deposits composed largely of raw humus.

According to Braun-Blanquet and Jenny (1926) alpine humus soils can be recognized by the fact that in their soil profile the A_1 horizon, consisting only of partly decomposed plant parts and windblown mineral matter, exceeds the other horizons. The difference between alpine humus, dry peat, and raw humus is only superficial, the chief criterion for raw humus being its acidity and its finely dispersed condition, which qualities are responsible for the unfavorable properties of unsaturated humus materials. Alpine humus soil is a genuine climatic type and eventually develops at high alpine altitudes irrespective of the geologic substratum, forming in considerable depth on lime as well as on crystalline rock. On lime the evolutionary process is much slower and more complicated. On crystalline rocks the weathered, disintegrated minerals with progressive humus formation and acidification proceed directly to the formation of alpine humus soil, the process being only a matter of time.

Most species of higher plants appear to have a considerable pH range within which they are able to carry on all their vital functions in a fairly normal manner. When other factors of the environment are favorable, the pH range is probably greatest. On tension lines between plant communities where soil water relations, humus content, and other factors are near their limits for certain species of the different communities, it is possible that

pH sometimes becomes the limiting factor in determining the distribution of species. A consideration of soil reaction values in different communities of the region (Table VI) shows that average pH values range from pH 5.0 to 6.4. The lowest soil reactions found were in lichen-moss snowflush community and in polsters on a fell field, where pH values of 4.0 and 4.2, respectively were obtained. Since most communities show soil reactions from pH 5.0 to 6.0, this factor does not appear to have any great significance directly in determining the distribution of the alpine plants in this region. Perhaps its greatest importance lies in its effect upon ionic exchange during the process of absorption of mineral salts and upon the promotion of the general nutrient-poor conditions of alpine soils by preventing the growth of soil organisms which would bring about a more complete decay of plant remains, thereby releasing the supply of nutrient materials bound up in the soil.

TABLE VI. *Soil reactions in alpine plant communities.*

Community	pH
Wind timber; also <i>Vaccinium</i> stands.....	5.2
Sedge moor.....	5.2
Wet sedge meadow.....	5.0
Snow flush.....	5.0
Fell field (Wind communities).....	5.0
Climax meadow (Elynetum).....	5.6
<i>Salix</i> (<i>S. chlorantha</i> , <i>S. pseudolapponum</i>).....	6.0
<i>Salix</i> (<i>S. nivalis</i> , <i>S. saximontana</i> , <i>S. petrophila</i>).....	4.8
<i>Dryas octopetala</i>	6.0
<i>Sedum rhodanthum</i> (Shallow streams, wet meadows)	6.0
Boulder field.....	6.0
Talus slide (no vegetation).....	6.4

Table VI summarizes the results obtained from many pH determinations made on soil of different plant communities of the region.

BIOTIC FACTORS

Grazing.—Grazing does not appear to have had a pronounced effect upon the alpine vegetation in this region, but no records are available for comparison of past and present conditions. Certain species of ruderals, *e.g.* *Polygonum aviculare*, *P. engelmanni*, *Chenopodium leptophyllum*, and *Capsella bursa-pastoris*, are found in a relatively limited area on the slopes of a valley used for a considerable number of years as a herder's camp. Sheep, cattle, and horses have frequently been gathered into this valley at nights during the grazing season. Since the plants just mentioned are unusual at this altitude and do not occur generally over the rest of the region, their occurrence is probably connected with the bringing of domestic animals into the area. Whether these species will persist or not remains to be seen. Cattle and horses were probably first brought up to these high altitudes during the early mining activity more than half a century ago. Some grazing has been carried on during summers for twenty or thirty years, but it is only during the last decade that anything like intensive grazing has been practiced.

Grazing by sheep is at present confined mainly to the region above the trees. Cattle graze mostly below tree line. Grazing by horses is at present in-extensive.

Due to the severity of conditions normally present, grazing might be accompanied by serious danger of upsetting the natural balance among species in the alpine region sooner than in regions with more favorable conditions for plant growth. In view of the limited extent to which intensive grazing has occurred on James Peak, it seems probable that it has had little influence upon alpine succession here.

Fire.—The effect of fire on vegetation in the alpine zone would be expected to be negligible. In the region about James Peak extensive fires destroyed a great deal of the forest in the subalpine zone in the decade from 1870-80. In places the burned areas extend to the alpine zone. Subalpine zone is potentially forest land while alpine zone is potentially grassland. Severe burning has removed forest and soil, and in exposed situations adjoining the former alpine-subalpine border, has resulted in conditions approximating those characteristic of alpine altitudes. Regeneration of the burned-over area has been slow. In much of the region few trees have appeared in the half century which has elapsed since the fire. On slopes exposed to severe wind action, many alpine pioneers have invaded the burned area, and alpine vegetation is now frequently encountered several hundred feet lower than the former alpine border. *Sieversia turbinata*, *Silene acaulis*, and *Eritrichium argenteum* are examples of distinctly alpine species now sometimes occurring as low as 10,600 feet, whereas the former timber line is at 11,000 to 11,500 feet. Patches of spruce, fir, and pine forest in a few places escaped the conflagration. These, as well as unburned stumps and prostrate tree trunks, give evidence of the former condition when subalpine forest covered the region and appear in striking contrast to the alpine aspect of the vegetation which sometimes surrounds them.

Clearing (lumbering), Mining.—Cutting of the trees has been almost negligible in its effect on the downward extension of the alpine zone. Had it not been for fire, which left little of the forest to attract the lumberman, this might have been otherwise as the region lying to the east and south of Kingston has been the site of considerable mining activity, which frequently levies a severe toll upon the surrounding forest. Since about 1900, however, mining activities have declined, and the demand upon what little forest escaped the fire has been slight.

VEGETATION

Introduction.—Alpine vegetation consists of the species characteristic of the alpine zone. True alpine plants are characterized by their ability to live in the open region above the trees. Tree species are able to succeed up to a certain height on a mountain slope. Beyond that limit grassland vege-

tation becomes dominant. The border between alpine and subalpine zones is itself commonly a belt of varying width in which these two different types of vegetation contend with one another and with the climate for existence and domination. With changes of climatic conditions this battle zone fluctuates up or down the mountain side. Various factors, such as exposure, slope, and soil, produce considerable differences in the altitude of the border line. There results a very irregular tension zone in which alpine and subalpine individuals and groups intermingle. This tension belt is a transition region between the two zones. It is commonly characterized by dwarfed, deformed tree species which tend to sprawl along the mountainside in the direction of the prevailing wind. This form of vegetation is variously known as wind timber, krummholz, or alpine scrub.

Below the tension zone the region comes eventually to be dominated by subalpine forests. Alpine species in many places have extended their ranges downward, perhaps only temporarily, in areas where fire, deep accumulation of snow, or severe wind have displaced subalpine plants. In places trees and other subalpine plants, aided by favorable conditions, have extended their ranges upward, crowding out, at least temporarily, alpine vegetation. Such fluctuations sometimes make it difficult to classify species as strictly alpine or subalpine. Throughout the present discussion the transition zone is treated as a part of the alpine. In the list of species found in the region plants appearing in the alpine zone only in the transition region are so indicated.

Alpine vegetation as a whole may be conveniently classified into the three distinct types of Schimper (1903): forest, grassland, and desert. The forest is represented only by the wind timber or alpine scrub forest of the transition zone and forms a more or less broken girdle varying greatly in width and in altitude. In this transition area occur alternately patches of scrub and of grassland, the former making up the greater part of the vegetation in the lower portion and the latter occupying the greater part near the upper margin. Where the borderline is approached on steep slopes or where it is marked by cliffs, the wind timber may be lacking and the change between zones may occur abruptly.

The greater part of the vegetation of the alpine zone is of the grassland type and occupies the broad and gentle mountain slopes and valleys above the tree limit. This treeless area is sometimes referred to as alpine tundra (Weaver and Clements 1929). Here occur the alpine meadows. The vegetation varies in floristic composition in accordance with the conditions of the particular habitat. It consists of grasses, sedges, dicotyledonous herbs, and in places it is dominated by shrubs. Seasonal aspects are pronounced at different times during the growing period. This grassland vegetation is best developed in the more favorable places and in its mature state is dominated by a sedge-grass climax.

Much of the alpine zone presents a rather barren aspect at all seasons. Due to the great extent of exposed rock and boulder heaps with little or no soil, much of the surface can, at best, support only a sparse vegetation of pioneer species. Portions of the region which are vegetationless or which possess only a very scant plant population fall within the category of alpine desert. Cliffs, hogbacks, talus slides, and boulder fields frequently extend the desert far below the alpine zone.

Methods.—The methods employed in this study of alpine vegetation and its succession are: (1) acquiring information concerning conditions existing at different stations or habitats throughout the region by instruments and by systematic and detailed observation; (2) determining the floristic composition of the vegetation in the various habitats and the relative abundance of the species in each association by means of a statistical study of the plant population of each habitat; and (3) reconstructing the complete course of vegetational development from its pioneer to its most advanced stages from a study of all these stages in places where they now occur in the region.

Data obtained from the study of the climatic factors were supplemented by observation of the changes taking place in the vegetation throughout the growing season. The results obtained and the conclusions reached from the study of the alpine environment are recounted in the preceding pages. The results of the floristic and successional studies are discussed in the succeeding part of this paper.

The analysis of the vegetation into its fundamental social or synecological units was effected principally by means of a modification of the statistical method as used by Raunkiaer (1918). This method of arriving at a knowledge of plants through a study of their community relationships has been used more extensively by European than by American ecologists. While the feeling is probably pretty general among Americans that some European phytosociologists have overemphasized the importance of the various social relationships in the development of plant communities, it must be admitted that the careful methods of analysis as practiced by central and northern European workers give an intimate knowledge concerning the exact structure and composition of the vegetation and its units and concerning the individual role and relative importance of each species in the community.

In this statistical study quadrats varying in size according to size of plants and density of vegetation were employed. For most of the alpine grassland where plants are small and occur in fairly uniform density, 0.1 square meter quadrats were employed. On fell fields and rock slides where the vegetation was sparse and it was desired to estimate proportion of bare surface as well as the frequency of species, 0.5 square meter was frequently the size used. One square meter was employed in studying dwarf shrub associations dominated by *Dryas*, *Ribes* spp., and the larger species of *Salix*. For the tree

species of wind timber a 10 meter quadrat was employed, but for the lower layers in this community the smaller units were used.

In each instance quadrats taken in linear series at uniform distances in places where the association appeared fairly uniform were scored for frequency of species, proportion of bare ground, and proportion of the area covered by each species if this coverage amounted to as much as one-twentieth of the whole. Due to the very prominent habit among alpine species of spreading vegetatively to form mats, cushions, or turf the proportion of the vegetation cover in a given habitat, furnished by a species, is far more significant in the matter of domination of the association than the number of individuals of this species present.

In order to facilitate the work of determining the importance of different species in an association from the standpoint of frequency or constancy of their occurrence, and of the proportion of the total area covered by each, the plan used by Braun-Blanquet and Pavillard (1925) was employed. Five degrees of presence or constancy, also five of covering or dominance are recognized. Each is expressed by the figures 1-5.

In regard to presence the significance is:

- 1, present in less than $1/5$ of quadrats studied
- 2, present in $1/5$ to $2/5$ of quadrats studied
- 3, present in $2/5$ to $3/5$ of quadrats studied
- 4, present in $3/5$ to $4/5$ of quadrats studied
- 5, present in $4/5$ to $5/5$ of quadrats studied

In regard to cover the significance is:

- 1, covering very feeble, less than $1/20$ of the area
- 2, covering $1/20$ to $1/4$ of the area
- 3, covering $1/4$ to $1/2$ of the area
- 4, covering $1/2$ to $3/4$ of the area
- 5, covering more than $3/4$ of the area

Attention was given to the matter of periodicity or seasonal prominence of different species, to layering, and to the fidelity or exclusiveness of species with regard to occurrence in one or more associations. Such facts help in arriving at the part played by each species and consequently in determining the importance of the species in the community.

ALPINE SCRUB FOREST; TENSION ZONE COMMUNITIES

The distribution of the alpine scrub in the transition region (Fig. 3) is ultimately determined as the result of the interplay of a complex of environmental factors. Of major importance are the amount of snow and its disposition by the wind. The presence or absence of the tree species appears frequently to be a matter of enough but not too much snow. Sufficient cover is required to protect the branches from the winter winds while the

ground is frozen. Except on rocks, spaces in the tension zone free from wind timber indicate either areas swept free from snow in winter or places where snow accumulates to such depth that the period after the snow melts is too brief to permit the necessary vegetative activities vital to the persistence of tree species. Seed need not be produced every year but must mature occasionally in some parts of the region. The sprawling habit of the woody species results from the weight of the winter snow and from the fact that all branches projecting above the snow are shorn off almost as if by a knife. As a rule, the shearing is an annual occurrence, but occasionally during a winter of deficient snowfall or of unusually severe winds large branches or



FIG. 3. Northeast slope of Kingston Peak. Looking upward across the wind timber zone showing the effect of wind and snow upon the distribution of alpine scrub. Snowflush areas (Schneetälchen) still contain considerable snow. Photographed July 3, 1928.

whole trees may be killed, producing the unsightly appearance frequently noticeable. Late frosts and dry summers add to the number of dead limbs. Fluctuations in amount of snowfall from year to year levy a serious toll upon the woody vegetation. The sand blast effect of wind driven ice crystals as well as the desiccating action of the wind is responsible for the unilateral development of the tree species so noticeable in both alpine and subalpine zones.

Evaporation rates in the shelter of the wind timber and in exposed openings alternating with the scrub, indicate differences in humidity, which are reflected in the varied floristic composition of the vegetation in the two habitats. Plants in the openings are the plants of the alpine meadows above. Plants

in the shelter of the wind timber form a society of less hardy species, many of which are common in subalpine forest below.

The wind timber community is dominated in its mature condition, in more favored locations with respect to snow accumulation, wind exposure, soil, and soil moisture, by a scrub climax of spruce-fir, *Picea engelmanni* and *Abies lasiocarpa*. Dry rocky slopes and windswept ridges, particularly with southwest exposure, are frequently dominated by *Pinus aristata* or *P. flexilis* which appear to form an edaphic climax in places almost destitute of soil and exposed to extreme desiccation by combined action of sun and wind. Where winter snow accumulation is more variable, *P. aristata* may sometimes be the only tree species present. In spruce-fir communities *Picea* appears to be the more resistant of the dominants. In less mesophytic parts of the community it constitutes a much larger part of the vegetation, sometimes forming almost pure stands. In more mesophytic locations it may give way to almost pure stands of *Abies*. In pine scrub the same relations hold between *P. aristata* and *P. flexilis*, the former dominating in places with more rigid life requirements. *P. aristata* rarely occurs on north slopes and never in wet locations. *P. flexilis* is much more generally distributed than *P. aristata* in the region and frequently extends downward well into the montane zone.

Thus the four prominent trees of the krummholz may be arranged in a series representing environmental conditions gradually increasing in severity as follows: *Abies lasiocarpa*, *Picea engelmanni*, *Pinus flexilis*, and *P. aristata*. As to their upper limits of distribution no consistent difference was observed. In the scrub forest as a whole spruce-fir constitutes a considerably greater proportion of the total area than does pine scrub, the latter constituting more of a fringe about areas occupied by krummholz and dominating locally in less favorable spots. While pine scrub may have acted as a pioneer in some places preceding the appearance of the spruce-fir, there are indications that in many places spruce has been the first of these tree species to invade the slope.

Straggling specimens of *Populus tremuloides*, *Juniperus communis sibirica*, and *Pinus murrayana* occasionally occur in the wind timber. *Pinus aristata* reaches its northernmost limit of distribution in this area and barely extends into the subalpine zone below the tension line to form a few groves of moderate sized trees.

Of first rank as determiners of conditions of the habitat in wind timber are the tree species. Considering the scrub forest area as a whole, species of the genus *Vaccinium* are probably next in importance in the maintenance of the community. The *Vaccinium* layer may be inconspicuous or entirely absent in many places, but this is usually true only in situations more extreme in regard to moisture or light. In much of the wind timber the lower layer is composed of a fairly well-developed carpet, varying in floristic

composition but dominated most frequently perhaps by species of *Vaccinium*. Quite often small openings between clumps or terraces of scrub also are dominated by *Vaccinium oreophilum* and *V. caespitosum*. Here as in much of the subalpine forest below the same relation appears to hold between the tree species and the accompanying under layer of *Vaccinium*. But there are many gaps in the *Vaccinium* society, and locally dominant in these in drier locations are *Polemonium pulcherrimum*, *Chamaenerion angustifolium*, and *Arnica cordifolia*. In the extreme outer edges of the wind timber mats may occur a zonation of *Carex siccata*, several grasses, and many other herbaceous species. Species characteristic of more mesophytic locations are *Pyrola secunda*, *Mertensia ciliata*, *Moneses uniflora*, *Adoxa moschatellina*, *Angelica grayi*, and *Erigeron salsuginosus*. Where shade is rather dense and fallen leaves of conifers form a humid substratum, species of mosses and *Peltigera aphthosa* frequently form a ground layer. The reaction of the soil layer under the krummholz is commonly about pH 5.2. Another shrub layer is frequently more or less distinguishable from the wind timber cover above and the *Vaccinium* layer below. In drier locations *Salix pseudolapponum* and *Ribes montigenum* develop more noticeably about the outer portions of the wind timber patches; and in wet places between clumps *Salix chlorophylla* and *Ribes coloradoense* frequently occur. With the more vigorous development of these shrubs the lower layers are much reduced.

On wet terraces, which sometimes alternate with the strips of wind timber, sedge moors occasionally develop. On the other hand, exposed openings in the wind timber may exhibit well developed alpine dry meadow vegetation, or if in rocky, windswept situations they may be almost barren, containing only xerophytic species of the fell fields above the tree limit or stands of *Dryas octopetala*, a dwarf shrub of the lower portions of the alpine zone.

Thus it will be seen that the vegetation of this tension zone is a complex in which can be recognized associations of alpine and subalpine zones; and it affords many examples of mixed vegetation representing transitional or tensional communities intermediate in floristic composition between distinctly alpine and subalpine vegetation.

It is of interest to note that here at the extreme upper limit of their range certain species, such as *Carex siccata*, *Chamaenerion angustifolium*, and *Aquilegia coerulea*, which at lower altitudes are characteristic of open areas, occur only in the shelter of wind timber or rocks.

ALPINE DESERT; PIONEER COMMUNITIES

Alpine desert occupies portions of the region which are entirely barren or possess only a sparse vegetation. Under this category are included bare rock surfaces, boulder fields, talus slides, fell fields, and places where late lying snow prevents the growth of plants. Instability of substratum, extreme exposure, low temperature, or unfavorable soil, water, and light re-

lations may be responsible for the continued barrenness. Bare rock surfaces present extreme conditions for plant life. Unstable talus slides are frequently more barren than the surfaces of stable rocks.

"Boulder fields" as here used signifies masses of rocks of various sizes, piled promiscuously but in relatively stable condition. Talus slides are masses of rocks of any size occupying the steeper mountain sides. They are usually in unstable condition, but in mature stages they may become stabilized by vegetation forming meadows where the talus consists chiefly of gravel or finer material. Fell fields are stable rocky areas exposing a considerable proportion of rock surface upon which higher vascular plants are unable to grow. The fell field presents a more even surface so its plants are more uniformly exposed than the vegetation of the uneven boulder field. It will be seen that in all these topographical units which make up the alpine desert the barrenness is outstanding. When vegetation becomes more plentiful, the area enters the category of alpine meadow.

The accuracy of results obtained by the statistical method of determining the floristic composition of the vegetation in a plant community depends largely upon the size of the unit used and on the uniformity of vegetation of the community. In the investigation of these barren areas only the fell field yielded satisfactory statistical data. This was due to lack of uniformity in distribution of the species belonging to any one community which was in turn due to the fact that different habitats frequently occur in such close proximity. Especially is this true of the boulder field. On the rocks themselves the most extreme conditions prevail. In the shelter of the boulders are protected habitats. Water drains from the surfaces of the rocks into cracks where very mesic conditions obtain. Thus the boulder field does not possess a uniform vegetation, but a variety of species from widely different plant associations, the whole constituting a vegetation mosaic. If a small unit is used in analyzing this vegetation, no constants will be found. If a large one is used, the list of constants will include almost all the species on the boulder field. In neither case will the results of the analysis reveal the associations, constants, nor the relative importance of the species which make up the associations. However, the boulder field constitutes a convenient topographical unit for the study of the high mountain region.

Boulder fields.—The xerosere on rocks begins with extremely xerophytic lichens of the genera *Lecanora* and *Rhizocarpon*. These are followed by less xerophytic types, such as *Parmelia*, which tend to overspread and replace preceding species. Irregularities and depressions are etched in the rock surfaces as a result of the dissolving action of substances formed by the plants. Decaying plant remains are added to the substratum, lessening the extreme dryness of the habitat. Low growing, xerophytic mosses in time appear among the lichens and gradually displace them. Accumulations of humus and disintegrating, wind blown rock particles in cracks and crevices,

as well as moss pads, furnish germinating beds for disseminules of vascular species. These pioneer vascular plants find lodgment either on materials deposited on rock surfaces or in cracks and crevices down in the rock itself. The latter positions are less exposed; and species having extremely low humus requirements become established in them. Relative insolubility of silicate rocks limits crevice development, and crevice communities are poorly represented in the region. The following species are commonly found on barren rocks, in cracks, or on ledges where little soil is apparent: *Tonestus pygmaeus*, *Saxifraga caespitosa*, *Primula angustifolia*, *Synthyris alpina*, *Androsace subumbellata*, *Luzula spicata*, *Heuchera parvifolia*, *H. bracteata*, and *Oxyria digyna*.

Certain species show remarkable ability to establish and maintain themselves among large boulders, forcing their way through narrow cracks among coarse fragments of eroded granite, seemingly in the absence of humus. Some of these are: *Claytonia megarrhiza*, *Synthyris alpina*, *Senecio carthamoides*, *Polemonium confertum*, and *Aquilegia saximontana*. Less exposed boulder slopes near alpine-subalpine border may possess a vegetation in which *Aquilegia coerulea*, *Mertensia ovata*, *Sieversia turbinata*, and species of *Carex* are conspicuous.

Evaporation data taken on a boulder field give little notion concerning water requirements of different plants making up the vegetation. Lichens on bare rocks exposed to desiccation by wind and sun must be extreme xerophytes. Many seed plants too, in exposed positions, with little or no soil accumulation, are pronounced xerophytes. Cushion or mat-forming species characteristic of wind communities on the fell field frequently occur in these exposed locations. But down in the shelter of boulders, especially in positions where water from sloping rock surfaces drains to them during rains, occur mesophytic species such as: *Viola biflora*, *Aquilegia coerulea*, *Sedum integrifolium*, *Carex chalciolepis*, *C. nova*, and *C. scopulorum*. The last two species are characteristic of wet alpine meadow or of sedge moor associations. In certain places where conditions of light, water, and soil accumulation are favorable, bits of alpine meadow containing species of the alpine climax vegetation may rarely be encountered among embedded boulders. This usually denotes an advanced stage in the development of the boulder field. Erosion and decomposition resulting from the combined action of climate and vegetation tend to wear down the projecting rocks, and where the action of wind and water are not too severe, the accumulation of erosion products and plant remains tends to fill the spaces between the rocks. Vegetation spreads and stabilizes the accumulating products. It appears possible that in the course of time, portions of a boulder field might be transformed to alpine meadow; or where exposure is so severe that the products formed can not accumulate and the barrenness remains, the boulder field might be transformed to fell field with the more uniform and distinctive

type of vegetation of the latter. Boulder fields on the southwest slopes of Kingston Peak suggest the latter type of transformation, while slopes with northern exposure or with shelter from wind occasionally suggest the possibility of the former type. Several species which come to be prominent with increasing density of plant population among the boulders are: *Sieversia turbinata*, *Claytonia megarrhiza*, *Festuca brachyphylla*, *Carex rupestris*, *Poa rupicola*, and *P. pattersoni*. One or more of these or of a considerable number of other species may assume the leading role at different stages in the succession on the boulder field, but probably no other species does this as frequently and under as widely different conditions as does *Sieversia turbinata*. It appears relatively early among the boulders, has a wide distribution, and succeeds under great variations of exposure and of water, light, and soil relations. During late stages where the boulder field appears to



FIG. 4. Windswept fell field on southwest slope at 12,100 feet showing cushion-mat vegetation. *Trifolium nanum*, *Arenaria sajanensis*, *Paronychia pulvinata*, *Silene acaulis* overspreading the rocks.

be undergoing transformation to meadow *Sieversia* is frequently the dominant element in the vegetation.

The soil reaction in the various communities occurring among the boulders varies from the slight acidity of the coarse grained granite particles in the absence of humus to the strongly acid reaction of the humus polsters. Determinations made showed a range from pH 6.2 to 4.8.

Fell fields.—Rock rather than vegetation frequently constitutes the greater part of the fell fields. Due to evenness of surface more uniform conditions of exposure prevail than on the boulder field. Stable rock sur-

faces frequently display an abundant flora of xerophytic rock lichens. Well known wind communities (Fig. 4) reach their most striking development on windswept ridges in the mountains. Polster and mat forms, rarely growing more than two or three inches high and presenting a closely shorn appearance, are characteristic of the vegetation in such locations. Several species share extensively and sometimes rather equally the exposed surface in wind communities on James Peak. *Arenaria sajanensis*, *Paronychia pulvinata*, *Trifolium nanum*, and *Silene acaulis* may dominate individually or jointly although several other species are characteristic of this community. Warming (1909) gives an excellent description of fell field vegetation. Because of severe exposure, plants with upright habit, unless extremely reduced in stature, rarely succeed in this habitat. Rosette plants, such as *Claytonia megarrhiza*, *Draba streptocarpa*, and *Saxifraga flagellaris*, are usually present. Grasses and sedges are not prominent but may occur where projecting rocks furnish shelter. The small sedge, *Carex rupestris*, is quite frequently found in these wind communities where it may not exceed an inch in height and rarely appears to fruit. Its ability to spread by rhizomes enables it to maintain itself.

Table VII shows the results of statistical analyses of three typical fell fields. In this, as in succeeding tables, prepared in similar manner to determine the floristic composition of various plant communities, the degrees of presence or constancy, and of dominance or cover are expressed in the columns opposite each species by means of the scheme previously explained. In each column the number preceding the period indicates the constancy and that following expresses the cover or dominance of the species. In case a species is present in any stand but does not occur frequently enough to deserve a rating, it is marked (+). A species occurring in some stands of a given type of community but not in others is marked (—) in the stands in which it is not represented. (Braun-Blanquet. 1932. pp. 68-72).

The evaporation rate on a rather barren fell field at 12,000 feet on Kingston Peak, southwest exposure, was 46.5 cc. per day throughout the period from July 10 to August 26, 1928. This station gave the highest evaporation rate found at any point in the alpine zone and reached an average of 58.4 cc. per day for 10 days from August 17 to August 26. The low cushion or mat form of compact stems greatly reduces the surface exposed to the desiccating action of the wind and also helps to stabilize the substratum and permits accumulation of humus and mineral particles in the interior of the cushion or mat. This sparsely populated plant community constitutes an edaphic climax on the exposed ridges and slopes in many places and may be expected to perpetuate itself as long as climate and soil conditions remain as they are at present. The soil reaction in this community is relatively strongly acid for the region, averaging pH 5.0 and sometimes reaching pH 4.8 to 4.4.

Talus slides.—Talus slides in unstable condition may be without vegetation, even lichens being absent from the shifting rocks. But where, due to moderate slope or to slight addition of material at the source of the slide, the disturbance is decreased, plants with low humus requirement and with special adaptation to the unstable substratum may appear. Certain species with extensively developed root systems and remarkable powers of vegeta-

TABLE VII—*Fell field associations*

Number of stands	1	2	3
Size of sample	15 sq. M	15 sq. M	15 sq. M
Number of samples scored	30	30	50
Altitude	13,000	11,500	12,500
Exposure	W	NW	SF
Slope	4°	12°	10°
Wind influence	extreme	exposed	exposed
pH of root layer	—	4.2	4.6
Vegetation cover %	30	40	33
<i>Arenaria salmonensis</i>	5.2	5.2	5.2
<i>Paranephria pulvinata</i>	5.2	5.2	5.2
<i>Trifolium nanum</i>	5.2	5.2	+
<i>Tonestus pygmaeus</i>	3.1	5.1	5.1
<i>Festuca brachypylla</i>	5.1	4.1	5.1
<i>Sisymbria tibbinata</i>	3.1	3.1	5.2
<i>Silene acaulis</i>	5.1	2.1	2.1
<i>Artemisia patteronii</i>	—	5.1	5.1
<i>Selaginella densa</i>	5.1	2.1	+
<i>Clavtonia megarrhiza</i>	3.1	5.1	—
<i>Carex rupestris</i>	2.1	+	2.1
Lichens spp.	5.1	+	5.1
Moss spp.	5.1	—	+
<i>Tritidum dasylethum</i>	—	2.1	5.1
<i>Eritrichium argenteum</i>	+	+	1.1
<i>Draba streptocarpa</i>	+	1.1	1.1
<i>Palax caespitosa</i>	—	2.1	+
<i>Saxifraga flagellaris</i>	1.1	2.1	—
<i>Poa rupestris</i>	+	+	+
<i>Luzula spicata</i>	3.1	1.1	—
<i>Lixodia serotina</i>	—	1.1	2.1
<i>Artemisia scopulorum</i>	+	—	1.1
<i>Oreoxis alpina</i>	—	+	1.1
<i>Sedum tempestivum</i>	+	—	2.1
<i>Elvina bellardi</i>	+	+	—
<i>Saxifraga chrysantha</i>	3.1	—	—
<i>Erigeron pinnatifidus</i>	—	—	2.1
<i>Primula angustifolia</i>	1.1	—	—
<i>Synthlipsis alpina</i>	1.1	—	—
<i>Androsace subumbellata</i>	+	—	—
<i>Cerastium beeringianum</i>	+	—	—
<i>Ischium montanum</i>	+	—	—
<i>Saxifraga caespitosa</i>	1.1	—	—
<i>Erismum nival</i>	+	+	—
<i>Senecio taraxacoides</i>	—	+	—
<i>Calamagrostis ptilopetala</i>	—	—	+
<i>Heuchera parvifolia</i>	—	+	—
<i>Actinea lanata</i>	—	—	+
<i>Castilleja occidentalis</i>	—	—	+
<i>Heuchera tenella</i>	—	+	—
<i>Saxifraga austromontana</i>	—	+	—

tive reproduction are sometimes of local occurrence on these talus slides. The plants sometimes anchor themselves by one or more deep roots extending a considerable distance downward into the more permanent material below and have a rather temporary but extensive root development in the superficial layer of less stable rock waste. The floristic analysis of a slide community usually shows few species even in a fairly well populated community. Great talus slides occur along the sides of Mammoth Gulch, sometimes extending downward for a vertical distance of almost a thousand feet. At certain points on these slopes specialized slide communities are well developed. Two species, *Chamaenerion latifolium* and *Chaenactis alpina*, were found nowhere in the region except on these slides where they sometimes dominated considerable areas almost exclusively on fine talus in relatively unstable condition. Other species commonly occurring on talus slides in less disturbed spots are: *Senecio holmii*, *S. taraxacoides*, *Polemonium confertum*, *Cerastium beeringianum*, and *Trisetum spicatum*. A limited number of determinations made on the talus slides showed a soil reaction of about pH 6.4. Since plants were very limited in number and there appeared to be no humus present, this reaction would appear to be nearly that due to the decomposition products of the rocks themselves independent of the vegetation.

ALPINE GRASSLAND; ALPINE MEADOW COMMUNITIES

Alpine grassland in the broadest sense includes all the region above timberline which under the present climate will eventually bear a grassland type of vegetation. Thus all the region with a growing season sufficiently long for the maintenance of the flowering plants becomes potential grassland. No place in the Colorado Mountains is too high to support many such species; and in all the areas studied, except unstable slides and stations where snow lies late or where north exposures result in extremely low light intensity, an active vegetation was found. However, there are many places where conditions for plant growth are so severe that an equilibrium between the forces of vegetation and climate appears to have been reached. Gains made by either in one place are offset by losses in another. Where such an impasse is due to certain long enduring conditions of the soil, we have edaphic vegetation types.

According to our modern view soil itself is a product of the climate and undergoes a cycle of evolution similar to that of the vegetation. At each stage in the cycle, soil and vegetation keep pace (Braun-Blanquet, 1932 pp. 255-260). Where soil development is retarded for long periods of time in its progress toward maturity, vegetation likewise is prevented from moving forward to its final or climatic climax condition. In a region as youthful as the Rocky Mountains where forces of erosion are still so active and general instability is so great, it is not surprising that in many places little progress has been made in the development of soil or vegetation.

In accordance with the scheme of classification the meager plant covering of barren rocky areas has been treated as alpine desert. The vegetation here described under alpine grassland consists largely of a series of developmental stages of low herbaceous vegetation frequently referred to as alpine meadow. In these stages plants have come to occupy at least a fairly large proportion of the total surface of the substratum, and the vegetation is characteristically dominated by species of grasses, sedges, and herbaceous plants. Communities dominated by woody species, constituting a scrub vegetation, are not infrequently encountered in different parts of the alpine meadow, and under certain conditions these appear to form an edaphic climax within the grassland area. Other distinctive edaphic communities which occur in the alpine zone are the snow flush meadow and sedge moor.

Several rather definite types of alpine meadow can be distinguished according to the soil moisture condition and to the length of growing season in different places. Where snow lies during all but a few weeks of the summer and the soil is kept saturated with cold water, snow flush communities persist. Where the soil is saturated with water but absence of snow permits a longer growing season of milder temperature, wet meadows or moors with luxuriant vegetation of hydrophytes occur. In places where water relations are favorable during a considerable part of the season but the soil undergoes aeration, the vegetation consists of plants of moderate water requirements and forms a mesophytic meadow. On exposed slopes or in any location where soil moisture is deficient, only plants with low water requirement can grow.

Much of the high mountain region falls into this last category, and the best vegetation possible appears to be a dry meadow composed of xerophytes. As with the wet meadows, two different vegetation types, depending primarily on soil moisture relations, can be distinguished in the dry meadows. The first is the rather sparse meadow, which sometimes appears to be a late stage of development of exposed fell and boulder fields. The second is the somewhat less xerophytic Elynetum or sedge meadow which has been reached on certain of the more stabilized slopes of the mountains. This type appears to be the ultimate or climax vegetation for a large proportion of the region.

Scrub associations.—The woody plants occurring in the alpine zone above timberline include various species of shrubs from several distinct communities growing under widely different environmental conditions. Species of *Salix* are common in wet stations in all but the higher alpine altitudes. Willows frequently play a part in some stage of development of alpine moor and snow flush floras. Dry stony slopes from timberline to 12,000 feet are often dominated by the low prostrate shrub *Dryas octopetala*; less frequently by clumps of *Dasiophora fruticosa*.

Salix scrub.—Alpine species of *Salix* can tolerate the severe conditions far above timberline because of ability to endure long submergence in cold

water, to root deeply and extensively, and to complete their life cycle from bud to seed in so short a period. Distribution of the different species is determined chiefly by their different requirements for water and for protection against winter winds. Diminutive species grow where there is insufficient water and winter snow cover for the taller species. All require at least a moist substratum. *Salix petrophila*, *S. saximontana*, and *S. nivalis* rarely exceed 2 to 3 inches in height. They occur on moist gravel slopes and terraces or along stony margins of streams or lakes. They thrive among coarse rock fragments with almost no soil. In such locations they meet little competition with other plants and often form continuous mats. Studded with buds their prostrate stems creep along the surface or burrow beneath the substratum, rooting everywhere. In summer each bud sends up its tiny shoot bearing several leaves and one or two catkins.

Salix monica is slightly taller reaching 6 to 10 inches. This species occurs about the borders of shallow water basins on stony terraces. These depressions hold sufficient snow to cover the stems during winter. *Salix chlorophylla* and *S. pseudolapponum* frequently grow 3 to 4 feet tall in the wind timber where they are most abundant. *S. chlorophylla* grows only about water but *S. pseudolapponum* may occur in any mesic situation since it has by far the lowest water requirement of all these willows.

Salix chlorophylla is usually restricted to the wind timber zone; *S. monica* occurs only above timberline at 11,500 to 12,000 feet. *S. nivalis* is rare. *S. pseudolapponum*, *S. petrophila*, and *S. saximontana* are common from 11,000 to 12,000 feet. In the shelter of the scrub thickets carpets of moss and flowering plants frequently develop. *Salix* scrub probably represents an edaphic community of long duration on coarse wet gravels in much of the alpine zone. Soil reactions in this community vary from pH 4.8 to 5.6.

In a few locations and always very limited in extent, patches of *Vaccinium oreophilum* are encountered in the alpine meadow above tree line. An extreme case was in a snow pocket at 12,000 feet on a sheltered slope more than 1,000 feet higher than the nearest wind timber a mile away. The occurrence of *Vaccinium* above the wind timber always appears to be dependent upon a snow cover which melts off by July 1. With such a short growing season it does not thrive; and as it rarely has time to mature seed, it spreads very slowly. Soil reaction in the *Vaccinium* community averages pH. 5.2.

Dryas scrub.—In the lower alpine zone stony slopes with a limited snow cover in winter but with exposure to wind in summer are often dominated by the small shrub, *Dryas octopetala*. In the wind timber zone insufficient snow accumulation frequently prevents tree species from occupying these slopes. Extreme exposure to wind during summer makes conditions difficult for herbaceous species. The slopes frequently present an irregularly terraced appearance because the shrubby plants tend to stabilize the gravel which is blown or washed down from higher levels. The terracing is probably partly

connected with the creep of the loose surface material down the slope during the melting of snow and during heavy summer showers. Deep rooting by *Dryas* holds it fast, but the creep inclines the clumps in the direction of movement. The stems of this dwarf shrub appear appressed to the sloping surface while the nearly level stony terrace tops alternate with small sloping *Dryas* clumps which form discontinuous strips running more or less horizontally along the slopes. Such an arrangement affords shelter from the wind and also makes possible the gaining of some heat by reflection from the rocky substratum. As a result this woody species is enabled to mature its seeds during the short growing period.

The *Dryas* stand is an open one; and while the shrub is dominant, it commonly has a considerable number of rather constant associates from pioneer rock communities and from the dry meadows. A population study of a typical *Dryas* slope shows the following species prominent: *Dryas octopetala*, *Carex rupestris*, *Actinea lanata*, *Arenaria sajanensis*, *A. aequicaulis*, *A. fendleri*, *Selaginella densa*, and *Eritrichium argenteum*. The *Dryas* association forms an edaphic climax on the exposed slopes and appears destined to persist as long as the conditions of wind, snow duration, and rocky soil remain as they are at present. In no case was *Dryas* found above 12,100 feet on James Peak. Soil reaction in this community was pH 6.0.

Dasiophora fruticosa occasionally occurs on exposed rocky slopes at timberline, and it ascends to 12,100 feet on Kingston Peak. In windswept positions it not infrequently assumes the rounded cushion form so characteristic of wind communities. In a few instances it forms stands capable of dominating the community in which it occurs.

Snow flush associations.—The term "Schneetälchen" was first used by Heer (1836) for localities in regions poor in calcium carbonate where the soil is kept saturated during much of the growing season by water from the late-melting snow cover. The characteristic vegetation in such places is a more or less dense stand of rather low growing turf or sod-forming species. Considerable study has been devoted to snow flush floras by central and northern European ecologists, but little attention has been given to them as definite plant communities of the alpine or arctic vegetation in North America.

Areas on James Peak from which snow usually does not melt before July 1 to 15 exhibit the characteristics peculiar to the snow flush. There appear to be two types of snow flush communities. Where the snow-free period does not exceed four or five weeks, the vegetation is sparse, usually consisting of mosses, lichens, and a few straggling grasses and sedges. Where the snow-free period amounts to six weeks or more, sedges, grasses, and several dicotyledonous herbs are also present. The latter type is much more clearly defined. It is frequently dominated by two or three species. Occasionally a single species forms almost a pure stand. *Carex nigricans* some-

times plays such a role. Other flowering plants prominent in these communities are: *Carex pyrenaica*, *C. nubicola*, *C. festivella*, *C. phaeocephala*, *C. festiva*, *Poa pattersoni*, *Aira caespitosa*, *Erigeron melanocephalus*, *E. uniflorus*, *Poa reflexa*, *Ranunculus adoneus*, *Sibbaldia procumbens*, *Trifolium parryi*, *Polygonum bistortoides*, *Sieversia turbinata*, and *Arenaria sajanensis*. The last two plants named above are of common occurrence in fell field and dry meadow. Such species are indifferent to snow cover in contrast to species which, like *Trifolium nanum*, seem to be restricted to the windswept fell fields.

Braun-Blanquet (1926) found that the plants composing the "Schneetälchen" flora of the Alps are species capable of carrying on their vegetative activities at a very low temperature, of completing their seasonal activity



FIG. 5. Snow flush community on east slope of Kingston Peak at 11,500 feet, dominated by *Aira caespitosa*, *Erigeron melanocephalus*, and *Carex nigricans*.

from bud to seed in a few weeks, and of propagating by vegetative methods since they are not permitted to produce a seed crop in some years. Annuals are never found in this community. Many of the plants pass the winter with green stems and leaves and carry on vegetative activity under the snow when the cover becomes thin in the early summer. On James Peak certain species, like *Ranunculus adoneus* and *Polygonum bistortoides*, not infrequently push their way through the thin snow cover.

Variation in the length of snow-free period in different snow flushes and propagation mainly by vegetative means by the first species to arrive in the habitat explain the frequent occurrence of almost pure stands as well as

the seeming lack of uniformity in floristic composition of different snow flush floras. Similarity of conditions in snow flush and wet meadow during the vernal aspect of the latter account for the presence of several of the same species in both.

The sod-forming species build up a thick layer of fine textured soil consisting of finely eroded minerals and a high percentage of humus. Soil reactions taken in several snow flush communities varied from pH 4.2 to 5.7. The more acid reactions occurred in a moss-lichen community at 12,200 feet.

With a growing season exceeding two months the water level recedes after the snow has all melted. Air enters the soil, the temperature rises, and different conditions develop in the habitat. Species requiring a longer growing season invade the community and replace the typical snow flush vegetation. However, as long as the snow-free period does not exceed two months and the cold water from the melting snow keeps the soil saturated during the most of this time, the snow flush vegetation will continue as edaphic plant communities dominated by the characteristic "Schneetälchen" flora.

Alpine moor associations.— The alpine sedge moor varies in floristic content according to the conditions under which it arises and the stage of its development. The absence from the alpine zone of certain plants, such as sphagnum, which are extremely important in the formation of extensive peat deposits in moors, is probably due to the severity of conditions during the growing season. Exposure to the desiccating action of wind in the absence of tall dense vegetation may be the limiting factor. Sedge moor is represented by sedge meadows which develop in stations watered by melting snow or by rains higher on the mountain. Water relations undergo considerable fluctuations during the season. One or more species of sedge may dominate a wet meadow, the resultant humus accumulation in time tending to bring about conditions resembling the moor. In most cases this development does not proceed very far. In locations more sheltered by surrounding topography or by the growth of the taller species of *Salix*, wind action is greatly lessened; and with more favorable and uniform water supply, species of mosses and sedges assume a more important role in the community. In time considerable accumulations of humus may result, with conditions more typical of the sedge moor. Species of *Salix* thus appear frequently to act as pioneers in such a community, helping to stabilize the coarse stony substratum in the beginning of the sere and to make possible later stages in its development.

Sedge moors are best developed along lake margins or along streams where the water supply is maintained more or less constantly. The vegetation tends to advance gradually into the water. A series of developing moors occurs on successive rock terraces near the outlet of James Peak Lake.

Species of *Carex* and *Juncus* have constructed restraining barriers at the lower edges of gently sloping terraces where the water spreads out in a thin sheet before falling to the next terrace below. Pools of water are formed on the terraces. The *Carex*-*Juncus* dike varies from a few inches to two feet in thickness, and the water seeps slowly through the humus barrier in many places or may overflow it after hard showers. *Carex aquatilis* appears to form most of the reinforcement for this dam; but *Juncus mertensianus* and *J. parryi* act as pioneers of the community. All these species form tenacious sods of underground organs by means of which the embankment is held in position. Mosses are prominent in the community. On the sloping sides of the narrow valley the vegetation shows a zonation from sedge-rush border at the water's edge to dry alpine meadow on the higher slopes. Overlapping but still distinguishable are the zones quite as described by Ramaley (1920) for high subalpine lake shore vegetation in the region several miles north of James Peak Lake. Mingling with the sedges are individuals of *Salix chlorophylla* and *S. pseudolapponum*. Where the water enters the uppermost basin, washing in more or less gravel, the following stream margin species occur: *Sedum rhodanthum*, *Cardamine cordifolia*, *Primula parryi*, *Epilobium lactiflorum*, *Juncus mertensianus*, and *J. parryi*. In the sedge community at slightly higher elevation are *Caltha rotundifolia*, *Trollius albiflorus*, *Pedicularis groenlandica*, *Gentiana romanzovii*, *G. monantha*, *Swertia congesta*, *Parnassia fimbriata*, and *Aira atropurpurea*, plants of the wet alpine meadow. In the sedge moor-wet meadow community also occur *Carex illota*, *C. misandra*, and *C. capillaris*. Representing the heath moor is a zone containing *Kalmia polifolia*, *Gaultheria humifusa*, and *Vaccinium caespitosum*. Species intermingling with the heath representatives and forming a transition to the upper slopes of dry alpine meadow are: *Aira caespitosa*, *Veronica alpina*, *Castilleja lauta*, *Potentilla diversifolia*, *Thalictrum alpinum*, and *Zygadenus elegans*.

Many species of the moors which develop in the transition zone on the alpine-subalpine border belong mainly to subalpine zone. It is apparent that conditions for the extensive sedge moor development are more favorable below than above timberline. James Peak Lake lies at 11,090 feet above sea level on the upper border of the transition zone. Alpine species dominate the exposed slopes in the vicinity while in sheltered places alpine and subalpine species intermingle. In the higher alpine altitudes of this region lakes are infrequent. Where they are present, snow and ice last so late that the growing season is too brief to permit the development of more than a sparse vegetation. Consequently, the nearest approach to the sedge moor on the high mountain slopes is usually the wet sedge meadow with its dense accumulation of peat-like material in the substratum. Echo Lake, which is located near James Peak Lake at practically the same altitude, is being in-

vaded in two or three places along its northern margin by a willow-sedge-heath moor formation similar to that just described.

Prominent species of the willow-sedge meadow moor of the higher altitudes are *Salix chlorophylla*, *S. pseudolapponum*, *S. monica*, *Carex nigricans*, *C. scopulorum*, *C. variabilis*, and several mosses. Species of less importance, but characteristic of the community are: *Artemisia scopulorum*, *Sicversia turbinata*, *Polygonum bistortoides*, *Sedum rhodanthum*, *Sedum integrifolium*, *Gentiana romanzovii*, *Castilleja occidentalis*, *Pedicularis scopulorum*, *Aira caespitosa*, *Festuca brachyphylla*, *Poa pattersoni*, *Juncus subtriflorus*, *Carex misandra*, and *C. capillaris*. One of the largest and best developed of these higher moors is on the southeast slope of James Peak, at 12,000 feet near the foot of a rather steep terrace which provides considerable shelter from the wind. The willows grow from one to three feet tall in a more or less closed formation, constituting a cover of about 50%. In a lower layer herbs and mosses form a ground cover of about 60% one third of which is mosses. *Carex nigricans*, *C. scopulorum*, and *C. variabilis* often perform a most important role in the formation of these moors on north exposures or in places where snow lies until July 1. *Carex nigricans* sometimes forms a close compact turf over the water saturated gravel substratum and dominates this association to the exclusion of almost all other species except mosses. With increased growing season the snow flush community sometimes tends to develop into a moor. The soil in moors and sedge meadows has a high humus content and a distinctly acid reaction varying from pH 4.8 to 5.8.

Wet meadow associations.—Border lines between plant communities are perhaps more poorly defined in the alpine zone than in any other region. The short growing season with its rapidly shifting conditions and the close proximity of widely different environments tend to complicate the situation. Embraced in the alpine flora within a relatively small area are most of the families and many of the genera occurring in a lowland region with a wide range of latitude and length of growing season. There is little wonder that this remarkable telescoping of latitudes, seasons, and vegetation into such a small space results in much overlapping of habitats and plant communities and frequently obscures distinctions which are easily observed at lower altitudes. In order to trace the succession it is necessary here as elsewhere to analyze the vegetation into its elementary units and to determine their relation to one another. Difficulty in defining these units frequently makes distinctions set up appear artificial and imaginary. Especially was this found to be true of the different communities and habitats of the hydrosere.

The wet alpine meadow consists of herbaceous species which thrive in soil saturated with water during all or most of their vegetative period. Algae and mosses are of frequent occurrence in streams and stagnant waters. No submerged aquatic flowering plants were observed. Probably few exist

in the cold waters. In lowland regions the vegetation of shallow stream and lake margins is frequently distinctly different floristically from that of the bordering shores even though the latter are water saturated; but at high altitudes in the mountains there is more uniform floristic structure in populations in wet places everywhere. Typical *Scirpus*-*Phragmites*-*Typha* stands do not reach the alpine zone. The nearest approach to such a stage of development is that occurring early in the formation of a sedge moor when a



FIG. 6. Wet meadow community along stream margin dominated extensively by *Mertensia ciliata*, *Primula parryi*, and *Aira caespitosa*.

border of *Juncus* species sometimes appears. But even this really belongs to the subalpine zone, rarely proceeding across the alpine-subalpine border. Such species as *Cardamine cordifolia*, *Sedum rhodanthum*, *Saxifraga arguta*, *Primula parryi*, *Mertensia ciliata*, *Pedicularis groenlandica*, and *Parnassia fimbriata* sometimes form almost pure stands confined to shallow streams and lake margins (Fig. 6). These may almost be considered to form an aquatic community. The volumes of most streams and lakes of the James Peak region are so changeable that little opportunity is afforded for such

stands to develop extensively; and since these same species occur mingled with the other species of the wet meadow about springs and seepage spots, they scarcely seem to form a distinct community.

In spite of rather obvious differences between wet meadow, snow flush, and alpine moor, the similarity of conditions existing in all three of these communities is indicated by the considerable number of species common to two or to all of them. Following are some examples: *Caltha rotundifolia*, *Trollius albiflorus*, *Ranunculus adoneus*, *Primula parryi*, *Polygonum bistortoides*, *Trifolium parryi*, *Carex scopulorum*, *C. variabilis*, *Poa alpina*, and *Aira caespitosa*. Several of these are also prominent in the mesophytic meadow. Environmentally the wet meadow differs from the snow flush in possessing longer growing season, higher temperature during the vegetative period, lower humus content and higher mineral content in the soil, and lower acidity. Wet meadow differs from alpine moor in the last three of these conditions. Floristically wet meadow commonly differs from both these other wet communities in its smaller proportion of grasses and sedges; but there are exceptions. Many species of the wet meadow require a longer growing season than is afforded by the snow flush, and many mature a seed crop during most years. The plants cannot carry on vegetative activities vigorously at such low temperatures as can many snow flush species. Reasons for the lower humus content in the soil of the wet meadow community may be in part less favorable conditions for accumulation of humus in actively flowing water and in part more favorable conditions for the washing in of mineral matter. More rapid destruction of humus may also occur since conditions are more favorable for the activity of bacteria than in the colder snow flush and in the more acid moor. A great difference occurs between the end conditions arrived at by the succession in the wet meadow and in these other wet communities. With building up of the substratum there occurs a lowering of the water table, and wet meadow proceeds directly and continuously through mesophytic meadow and arrives at the climax vegetation of the region. But as long as the climate of the region remains as at present, snow flush and alpine moor, because of peculiar local conditions imposed upon them, appear destined to retain their characteristic types of vegetation.

The volume of alpine streams varies greatly not only at different times of the season but frequently during the course of the day. Many small streams flow continuously during the early part of the season while the snow is melting but in late summer only during periods of frequent showers. A study of the flora about the margin of a stream or lake of variable volume shows a community of species of high water requirements in early summer, while many plants of low water requirements occupy the same location in late summer. Such variable conditions are not limited to stream and lake side. Population studies in several communities repeatedly show well defined

hydrophytes, mesophytes, and even species common in dry habitats growing side by side in the same 0.1 square meter sample plot. Probably the hydrophyte has almost finished its vegetative activity before the xerophyte starts its season's growth.

Such pronounced variations in environmental conditions during the growing period help to bring about the seasonal aspect in the high mountains. Seasonal phases of the vegetation, which are quite distinct in regions with long growing seasons, follow one another in rapid succession in the brief vegetative period which occurs at high altitudes. While they can be distinguished in practically all alpine communities, the seasonal expressions are possibly more marked in the wet meadow than in any other one community. Fairly well defined vernal, summer, and autumnal facies can be distinguished. *Ranunculus adoneus* frequently springs into bloom before the snow has melted away from it; and other species, such as *Polygonum bistortoides* and *Caltha rotundifolia*, force their leafy shoots above the frozen soil, suggesting a prevernal stage. Soon after the snow melts away in June, *Pulsatilla hirsutissima*, *Lloydia serotina*, *Androsace subumbellata*, *Primula angustifolia*, *Eritrichium argenteum*, and *Synthyris alpina* are blooming on the slopes and ridges while *Caltha rotundifolia*, *Trollius albiflorus*, *Ranunculus alpeophilus*, and *Cardamine cordifolia* appear in the shallow water of streams or along their wet margins, giving a well marked vernal aspect to the vegetation of the wet meadow. During July while *Rydbergia grandiflora*, *Trifolium nanum*, *T. dasyphyllum*, *Actinea lanata*, *Sieversia turbinata*, *Arenaria sajanensis*, *Dryas octopetala*, and *Castilleja brachyantha* are blooming in the drier communities, *Sedum rhodanthum*, *Trifolium parryi*, *Saxifraga arguta*, *Sieversia turbinata*, *Polygonum bistortoides*, *Erigeron saluginosus glacialis*, *Senecio crocatus*, *Pedicularis groenlandica*, *Parnassia fimbriata*, *Mertensia ciliata*, *Viola bellidifolia*, and *Veronica alpina* give expression to the summer phase of the wet meadow.

In August the approach of autumn is announced by a rather monotonous tone over the drier parts of the alpine zone. However, the communities with more favorable water relations are still marked by a considerable display of blossoms. The wet meadow at this time is brightened by *Siwertia congesta*, *S. palustris*, *Gentiana monantha*, *G. plebeja holmii*, and *G. parryi*, all members of *Gentianaceae*. Species of grasses and sedges are often prominent in this community throughout the growing season because of the favorable water relations. Sometimes they may dominate the vegetation, but this happens less frequently and less completely than in moor and snow flush.

A study of a number of wet meadow populations in different parts of the alpine zone (Table VIII) shows that the domination of this type of community is shared by a considerable number of species, and those which dominate in one wet meadow may be almost or entirely absent from another. Part of this lack of uniformity in floristic composition is due to seasonal

TABLE VIII—*Wet meadow associations*

Number of stand.....	1	2	3	4
Size of sample.....	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored.....	20	20	40	20
Altitude.....	11,100	11,500	12,500	11,000
Exposure.....	NW	E	SE	F
Slope.....	8°	5°	12°	7°
Wind influence.....	slight	slight	medium	slight
pH of root layer.....		5.4	5.0	5.4
Vegetation cover %.....	90	90	95	90
<i>Sieversia turbinata</i>	3.2	+	5.3	5.2
<i>Aira caespitosa</i>	2.1	3.1	5.3	5.3
<i>Carex scopulorum</i>	3.1	5.3	2.1	2.1
<i>Polygonum bistortoides</i>	3.1	+	5.2	2.1
<i>Caltha rotundifolia</i>	5.2	5.3	5.2	2.2
<i>Gentiana romanowskii</i>	3.1	—	5.1	5.1
<i>Artemisia scopulorum</i>	4.2	—	5.1	5.1
<i>Trifolium parryi</i>	3.1	+	+	5.1
<i>Pedicularis groenlandica</i>	2.1	+	5.1	2.2
<i>Erigeron salsuginosus</i>	—	2.1	3.1	3.1
<i>Thalictrum alpinum</i>	5.1	—	—	1.1
Moss spp.....	+	5.1	5.1	+
<i>Festuca brachyphylla</i>	+	2.1	3.1	3.1
<i>Luzula spicata</i>	2.1	+	+	+
<i>Epilobium lactiflorum</i>	2.1	3.1	+	3.1
<i>Phleum alpinum</i>	—	3.1	+	1.1
<i>Veronica alpina</i>	+	3.1	—	1.1
<i>Trollius albiflorus</i>	2.1	+	—	3.1
<i>Senecio crocatus</i>	2.1	+	1.1	3.1
<i>Chondrophylla americana</i>	1.1	3.1	—	2.1
<i>Swertia congesta</i>	—	2.1	—	2.1
<i>Potentilla diversifolia</i>	3.1	+	—	3.1
<i>Angelica grayi</i>	2.1	1.1	—	—
<i>Gentiana plebeja</i>	3.1	—	—	+
<i>Gentiana monantha</i>	2.1	—	—	+
<i>Saxifraga arguta</i>	2.1	+	—	+
<i>Saxifraga austriaca</i>	+	+	—	+
<i>Lloydia serotina</i>	2.1	—	+	—
<i>Poa alpina</i>	—	2.1	—	—
<i>Stellaria longipes</i>	—	2.1	—	2.1
<i>Erigeron uniflorus</i>	2.1	—	1.1	—
<i>Erigeron melanocephalus</i>	2.1	+	+	—
<i>Viola bellidifolia</i>	2.1	—	—	+
<i>Cardamine cordifolia</i>	2.1	+	—	+
<i>Primula parryi</i>	2.1	+	—	+
<i>Carex nigricans</i>	—	2.1	—	+
<i>Sedum rhodanthum</i>	2.1	+	—	+
<i>Senecio triangularis</i>	2.1	+	—	+
<i>Mertensia ciliata</i>	+	—	—	+
<i>Ranunculus alpeophilus</i>	+	—	—	+
<i>Valeriana acutiloba</i>	2.1	—	—	+
<i>Sagina saginoides</i>	+	+	—	—
<i>Stellaria umbellata</i>	+	—	+	—
<i>Juncus parryi</i>	—	+	—	+
<i>Juncus subtriflorus</i>	—	+	—	+
<i>Juncus castaneus</i>	+	—	—	+
<i>Pedicularis grayi</i>	+	—	—	+
<i>Parnassia fimbriata</i>	—	—	—	+

shifting of borderlines between communities and to the fact that the population studies in the different locations were made at different times during the season. All species do not appear at the beginning of the growing period. Some complete their vegetative activity in a short time then die down and so may easily be missed in a study made later in the season. The following may be regarded as species which rank high in their importance and in the frequency of their occurrence in this community: *Caltha rotundifolia*, *Sieversia turbinata*, *Polygonum bistortoides*, *Gentiana romanzovii*, *Artemisia scopulorum*, *Aira caespitosa*, *Erigeron salsuginosus glacialis*, *Pedicularis groenlandica*, *Trifolium parryi*, *Epilobium lactiflorum*, *Festuca brachyphylla*, *Senecio crocatus*, and certain species of mosses.

Where conditions are favorable for deposition by water and wind, the soil layer is rather rapidly built up by accumulation of inorganic and organic deposits. With the sinking of the water level beneath the soil surface, species of plants with lower requirements invade the wet meadow community. Its population undergoes a change floristically, and characteristic hydrophytes gradually drop out. Species characteristic of the mesophytic meadow, and finally those of the climax vegetation, become prominent and in turn dominate the changing community.

Soil acidity determinations in a number of stream and lake margin communities with wet meadow floras gave results varying from pH 6.0 to 5.2

Mesophytic meadow associations.—Differing from the wet meadow in the water relations existing in the soil, this community frequently occurs as a transition stage between wet and dry meadow. Mesophytic meadows may occur on slopes in the midst of boulder fields, or they may be surrounded by climax or dry meadows in complete absence of wet meadow vegetation. Water from higher on the mountain probably comes close to the surface of the ground in these places. Slopes sheltered from the direct rays of the sun or from the wind are likely to be suited to the plants of this community, most of which do not endure long continued submergence of their root layer during the growing season. Exposed slopes are subjected to too excessive drying during much of the vegetative period.

Examples of mesophytic meadows on moderately exposed slopes occur on the northwest slopes of James and Parry Peaks at 13,000 feet (Fig. 7). Wind prevents extensive snow accumulation and northerly inclination tends to prevent extreme desiccation. The moist soil supports a rather luxuriant vegetation of the meadow type which is frequently dominated by *Poa patersoni*. *Sieversia turbinata*, *Claytonia megarrhiza*, *Gentiana romanzovii*, *Carex atrata*, *Juncus triglumis*, *Luzula spicata*, and *Synthyris alpina* are prominent while a number of pioneer species of adjoining boulder and fell fields are present apparently as "holdovers" from preceding stages of the succession. Slopes at similar altitude on southern or southwestern exposures are usually occupied by rather barren boulder or fell fields except along

streamsides. Eastern exposures are more likely to have considerable snow accumulations, and the type of community present depends upon rockiness of the slope and length of time it is free from snow.

In moist places at lower elevation in the alpine zone two types of mesophytic meadow are common. One of these frequently borders stream or lake margins and appears to be more or less in the nature of a transition stage in the succession intermediate between wet meadow or snow flush and the climax meadow community. The other occurs in places on dry slopes where water from higher on the mountain comes close to the surface and seepage areas may be present in early season. Prominent in both are cer-

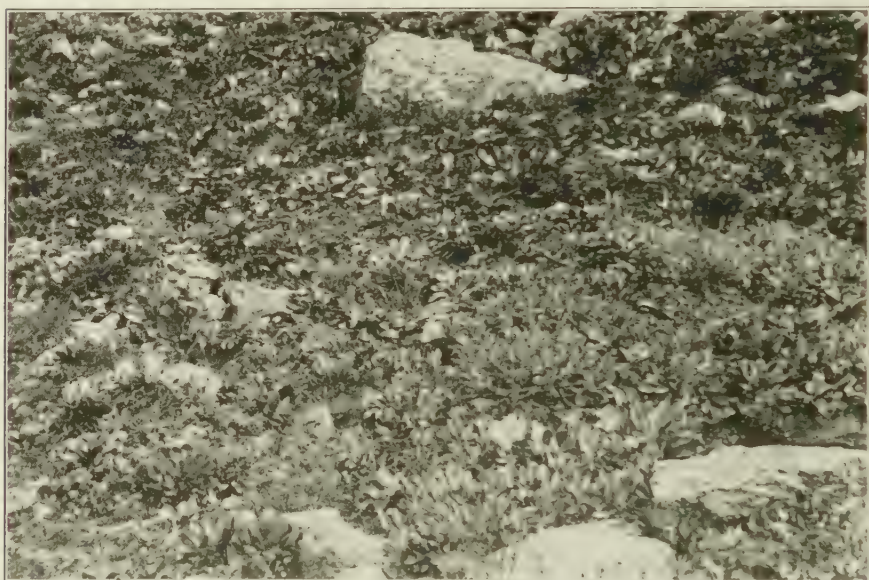


FIG. 7. Mesophytic meadow community on northwest slope of Parry Peak at 13,000 feet, dominated by *Claytonia megarrhiza*, *Gentiana romanzovii*, and *Poa pattersoni*.

tain species of sedges and such dicotyledons as *Sieversia turbinata*, *Polygonum bistortoides*, *Trifolium parryi*, *Artemisia scopulorum*, *Gentiana romanzovii*, *Potentilla diversifolia*, *Veronica alpina*, *Polygonum viviparum*, *Erigeron uniflorus*, and *Castilleja occidentalis*. On mesophytic rocky slopes which may represent late stages of a boulder field, *Aquilegia coerulea* is sometimes quite conspicuous along with sedges, *Sieversia turbinata*, and other species which give the community a meadow-like aspect. Sedges occurring in the mesophytic meadow are: *Carex nova*, *C. chalciolepis*, *C. atrata*, *C. misandra*, *C. capillaris*, *C. nigricans*, and *Elyna bellardi*. Mesophytic meadows, in locations more or less favorable for snow accumulation, tend to lose the characteristics distinguishing them from snow flush communities. Some of the species in this community may be regarded as "hold-

overs" from wet meadow in places where the latter has preceded the present stage of succession. On the other hand, where snow does not accumulate and soil water becomes deficient early, *Elyna bellardi* and other species of the climax meadow may constitute a considerable proportion of the vegetation.

In lower portions of the alpine zone and in openings among the wind timber one occasionally encounters mesophytic meadow of a still different type due to the presence of a considerable proportion of species of grasses which are either quite locally distributed or which seldom form stands sufficiently extensive to impress their stamp upon the community. *Aira caespitosa* and *Poa alpina* are likely to be present from preceding communities of the hydrosere. But on moderately mesophytic slopes grassy meadows are occasionally encountered in which one or a number of the following species are prominent: *Festuca brachyphylla*, *Trisetum spicatum*, *Phleum alpinum*, *Poa rupicola*, *P. grayana*, *P. reflexa*, *Agrostis hiemalis*, *Calamagrostis canadensis*, *Aira atropurpurea*, *Trisetum wolffi*, *Agropyron tenerum*, and *Festuca rubra*. These species may intermingle with the sedges and dicotyledons as a minor element, or at times they may dominate the community. *Festuca brachyphylla* and *Poa rupicola* are among the most widespread species of the alpine zone and appear in several communities, but they rarely form stands of any considerable extent. Mesophytic grassy meadows appear for the most part to be poorly developed in the alpine zone in the James Peak region and form a rather inconspicuous element in the vegetation. The Cyperaceae are of much greater significance than the grasses in the alpine succession in both hydro- and xero-seres.

Population studies made in five different mesophytic meadow communities are summarized in Table IX. These show that along with such species as *Polygonum bistortoides*, *P. viviparum*, *Trifolium parryi*, *Festuca brachyphylla*, *Poa alpina*, *Phleum alpinum*, *Trisetum spicatum*, *Potentilla diversifolia*, *Artemisia scopulorum*, and *Veronica alpina*, which perhaps reach their best development in this community, are a number of species characteristic of wet meadow and snow flush and several which are more characteristic of the climax meadow.

Gradual building up of the soil level and decrease in soil water are accompanied by the dropping out of the more mesophytic species and make possible the invasion of the community by plants of lower moisture requirement. In time *Elyna bellardi* usually appears, and as a result of the progressive dominance by invading species, the meadow assumes a less mesophytic and a more monotonous aspect. Less exposed slopes with short growing season or more favorable water relations may retain indefinitely the mesophytic element in their vegetation and may not yield to the invasion by *Elyna bellardi* and other climax meadow species. Soil reactions determined

TABLE IX—*Mesophytic meadow associations*

Number of stand.....	1	2	3	4	5
Size of sample.....	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored.....	30	20	20	30	20
Altitude.....	11,100	11,400	11,700	12,500	13,200
Exposure.....	NW	E	N	SE	N
Slope.....	10°	10°	30°	8°	20°
Wind influence.....	slight	moderate	slight	slight	moderate
pH of root layer.....	—	5.4	—	5.2	5.2
Vegetation cover %.....	90	90	100	95	80
<i>Sieversia turbinata</i>	5.3	3.1	5.3	5.1	5.3
<i>Trifolium parryi</i>	2.1	5.2	5.2	5.2	—
<i>Aira caespitosa</i>	2.1	5.3	2.1	5.2	—
<i>Polygonum bistortoides</i>	2.1	5.2	3.2	5.2	—
<i>Artemisia scopulorum</i>	4.1	3.1	5.1	5.2	5.1
<i>Gentiana romanzovii</i>	3.1	2.1	4.2	2.1	5.2
<i>Lloydia serotina</i>	3.1	2.2	5.1	3.1	—
<i>Polygonum viviparum</i>	5.2	3.1	5.2	—	—
<i>Poa alpina</i>	4.2	5.2	—	3.1	—
<i>Festuca brachyphylla</i>	3.1	2.1	4.1	3.1	2.1
<i>Thalictrum alpinum</i>	5.2	+	3.1	—	—
Moss spp.....	5.1	—	5.1	—	5.2
<i>Elyna bellardi</i>	2.1	2.1	3.1	1.1	+
<i>Trisetum spicatum</i>	+	2.1	2.1	1.1	—
<i>Erigeron uniflorus</i>	1.1	2.1	+	3.1	—
<i>Carex scopulorum</i>	4.2	—	2.1	3.1	—
<i>Potentilla diversifolia</i>	2.1	3.1	+	+	—
<i>Poa patersoni</i>	—	+	—	—	5.3
<i>Saxifraga chrysantha</i>	—	—	—	—	5.1
<i>Castilleja occidentalis</i>	1.1	—	2.1	2.1	—
<i>Primula angustifolia</i>	1.1	—	2.1	—	2.1
<i>Salix petrophila</i>	2.1	+	—	—	—
<i>Salix saximontana</i>	3.1	—	—	—	—
<i>Luzula spicata</i>	2.1	1.1	2.1	+	3.1
<i>Carex rupestris</i>	—	—	2.1	—	2.1
<i>Swertia congesta</i>	3.1	+	1.1	—	—
<i>Stellaria longipes</i>	1.1	+	2.1	—	—
<i>Erigeron melanocephalus</i>	—	3.1	—	3.1	—
<i>Veronica alpina</i>	1.1	2.1	2.1	—	—
<i>Draba crassifolia</i>	+	+	—	2.1	—
<i>Silene acaulis</i>	1.1	—	+	—	2.1
<i>Trifolium nanum</i>	+	—	+	—	2.1
<i>Gentiana plebeja</i>	3.1	+	+	—	—
<i>Phleum alpinum</i>	+	2.1	—	+	—
<i>Lewisia pygmaea</i>	—	—	—	2.1	1.1
<i>Arenaria sajanensis</i>	—	+	—	+	+
<i>Castilleja laeta</i>	+	—	—	—	—
<i>Castilleja rhexifolia</i>	+	+	—	—	—
<i>Chondrophylla americana</i>	3.1	+	—	—	—
<i>Solidago decembris</i>	—	2.1	—	—	—
<i>Erigeron salsuginosus</i>	—	2.1	+	—	—
<i>Carex misandra</i>	1.1	+	—	—	—
<i>Mertensia ovata</i>	2.1	2.1	—	—	—
<i>Gentiana monantha</i>	3.1	—	+	—	—
<i>Sibbaldia procumbens</i>	—	—	+	1.1	—
<i>Sedum integrifolium</i>	1.1	3.1	—	—	—
<i>Stellaria umbellata</i>	+	—	—	2.1	—
<i>Poa grayana</i>	+	+	—	—	—

in a number of mesophytic meadows varied from pH 5.0 to 6.0 and averaged about pH 5.4.

Dry meadow associations.—Even at its best a large proportion of the alpine zone appears capable of supporting only a rather poor vegetation. After long ages of struggle between the forces of climate and vegetation, exposed areas of any considerable relief commonly bear but a scanty, poorly developed soil and a meager and rather monotonous vegetation, which might be described as an impoverished dry meadow. The evaporation rate at a station maintained in this dry meadow at 11,500 feet, southwest exposure, was 36.7 cc. per day for the period from July 12 to August 25, 1928. During some weeks the daily rate was considerably higher. In view of the moisture conditions which must obtain in a coarse grained soil, poor in humus and spread in a thin layer on the rocky slopes, the effect of this high evaporation rate, during a week of rainless weather in late July, goes far toward explaining the scanty vegetation. In spite of a relatively high rainfall and humidity much of the region presents conditions for plant life approaching those of deserts in severity. Under the best conditions that can ultimately obtain the vegetation must therefore consist of plants adapted to xeric conditions.

The small sedge, *Carex rupestris*, possesses to a remarkable degree the qualities necessary for success under these rigid conditions. Small size and xerophytic structure give it a low water requirement. The habit of rooting deeply and branching underground enables it to secure moisture and to stabilize its habitat. Low humus requirement permits it to come as a pioneer into the habitat, and vigorous vegetative activity enables it to spread quickly. It requires no snow protection, so on sunny slopes it has the full season for vegetative propagation. Low stature, upright habit, and the tiny space it requires, enable it to succeed in the closely appressed vegetation of wind communities or among the thin stands of somewhat taller vegetation of less exposed stations. *Carex rupestris* occurs on boulder field, on stable slides, on fell fields, in *Dryas* communities, and is a constant species in dry meadow and in poorer parts of the climax alpine meadow. Except for the very beginning of the xerarch succession on bare rock, this species persists throughout the xerarch sere, and while never found in wet communities, it sometimes occurs in mesophytic meadows kept free from snow cover.

Probably next in importance in the dry meadow community is *Sieversia turbinata*. It too appears adapted for withstanding a wide range of environmental conditions. It appears on the boulder field, and while its larger size and upright habit render it less suited to exposed stations, it commonly occurs in all but the most exposed fell fields. The limiting factor in its distribution in several communities appears to be the snow cover. *Sieversia* apparently is favored by snow protection during the winter months and tolerates a covering to mid-July or possibly later. It is a good stabilizer and appears relatively indifferent to humus. Besides persisting throughout all but

the initial stage of the xerosere, it is also present in all stages of the hydrosere except in aquatic communities. *Sieversia* is a constituent of wet gravel communities dominated by *Salix* and remains important through all the later stages of the hydrosere. It frequently occupies a conspicuous place in the climax meadow in less extremely exposed situations.

While these two species have many associates, the latter vary greatly according to conditions existing in the habitat. Cushion-mat forming species are common, but *Carex rupestris* and *Sieversia turbinata* are of a high degree of constancy and of greatest constructive importance in this association (Fig. 8), which endures on dry slopes for long periods of time. Ultimately improved soil conditions lead to a somewhat less xerophytic meadow, which constitutes the climax vegetation for much of the region. The dry meadow then appears on exposed slopes as a transition



FIG. 8. Dry meadow. *Carex rupestris* and *Sieversia turbinata* invading a fell field and transforming it to the rather impoverished dry sedge meadow.

stage in the xerosere between the pioneer communities of the alpine desert and the climax sedge meadow. The particular type of community preceding it is frequently revealed by statistical analysis of the vegetation, as well as by indications from topography and surrounding associations. The plants making up the association consist largely of species from these pioneer communities although some newcomers appear on account of the changed conditions in this habitat.

Important species in the alpine dry meadow are: *Carex rupestris*, *Sieversia turbinata*, lichens, *Arenaria sajanensis*, *Elyna bellardi*, *Festuca brachyphylla*, *Eritrichium argenteum*, *Selaginella densa*, *Phlox caespitosa*, *Silene*

TABLE X—Dry meadow associations

Number of stand.....	1	2	3
Size of sample.....	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored.....	30	20	20
Altitude.....	12,500	11,700	11,500
Exposure.....	E	SW	SE
Slope.....	7°	10°	15°
Wind influence.....	strong	strong	strong
pH of root layer.....	4.6	5.2	5.6
Vegetation cover %.....	60	70	50
<i>Carex rupestris</i>	5.2	5.2	5.2
<i>Sieversia turbinata</i>	5.2	5.2	1.1
<i>Arenaria sajanensis</i>	5.2	5.2	5.2
<i>Silene acaulis</i>	3.2	5.2	1.1
<i>Paronychia pulvinata</i>	5.2	1.1	2.1
<i>Lloydia serotina</i>	3.1	5.1	5.1
<i>Artemisia pattersoni</i>	3.1	3.1	5.1
<i>Eritrichium argenteum</i>	2.1	5.1	3.1
<i>Selaginella densa</i>	2.1	5.1	2.1
<i>Phlox caespitosa</i>	1.1	5.1	2.1
<i>Trifolium dasyphyllum</i>	5.2	—	1.1
Lichen spp.....	5.1	5.1	5.1
<i>Festuca brachyphylla</i>	4.1	1.1	1.1
<i>Erigeron pinnatisectus</i>	4.1	3.1	+
<i>Polygonum viviparum</i>	—	5.1	1.1
<i>Oreoxis alpina</i>	3.1	3.1	2.1
<i>Tonestus pygmaeus</i>	4.1	—	2.1
<i>Actinea lanata</i>	1.1	3.1	4.1
<i>Luzula spicata</i>	3.1	2.1	+
<i>Artemisia scopulorum</i>	1.1	2.1	+
<i>Draba streptocarpa</i>	+	3.1	1.1
<i>Elyna bellardi</i>	+	2.1	3.1
<i>Calamagrostis purpurascens</i>	+	1.1	3.1
<i>Arenaria fendleri</i>	+	3.1	3.1
<i>Saxifraga rhomboidea</i>	—	4.1	+
<i>Poa rupicola</i>	2.1	1.1	2.1
<i>Campanula uniflora</i>	—	+	2.1
<i>Campanula rotundifolia</i>	1.1	—	2.1
<i>Potentilla saximontana</i>	—	+	2.1
<i>Allium pikeanum</i>	—	—	5.1
<i>Erysimum nicae</i>	—	+	+
<i>Arenaria aequicaulis</i>	—	—	2.1
<i>Castilleja brachyantha</i>	—	—	2.1
<i>Trifolium nanum</i>	—	1.1	—
<i>Primula angustifolia</i>	—	1.1	—
<i>Sedum stenopetalum</i>	1.1	—	—
<i>Avena mortoniana</i>	1.1	—	—
<i>Castilleja occidentalis</i>	1.1	—	—
<i>Rydbergia grandiflora</i>	+	+	—
<i>Thlaspi coloradoense</i>	1.1	+	—
<i>Agropyron tenerum</i>	+	—	—
<i>Sedum integrifolium</i>	+	—	—
<i>Dryas octopetala</i>	—	—	1.1
<i>Dasiophora fruticosa</i>	—	—	1.1

acaulis, *Saxifraga rhomboidea*, *Polygonum viviparum*, *Lloydia serotina*, *Artemisia pattersoni*, *Oreoxis alpina*, *Draba streptocarpa*, *Erigeron pinnatisectus*, *Actinea lanata*, *Artemisia scopulorum*, and *Poa rupicola*. In meadows with north exposure conditions are less severe due partly to winter snow

cover and partly to somewhat better moisture relations during the growing season. Here *Sieversia* and certain other plants are more prominent than on south or west exposures. Some species which play a much more important role in these protected stations are: certain mosses, *Sieversia turbinata*, *Festuca brachyphylla*, *Thalictrum alpinum*, *Luzula spicata*, *Polygonum viviparum*. *Carex rupestris* and *Elyna bellardi* may be present. Soil reactions in many dry meadow communities show an average acidity of pH 5.6. Table X summarizes population studies made in three typical dry meadow associations.

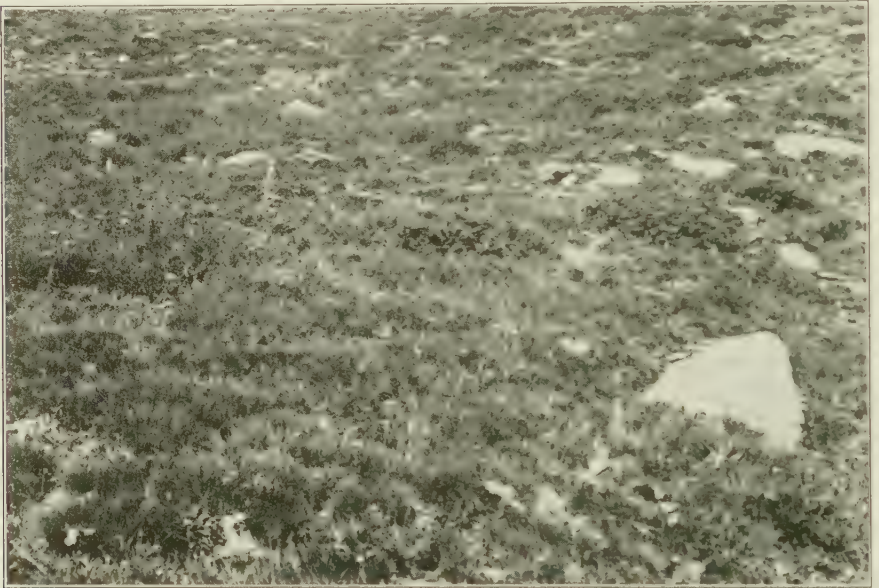


FIG. 9. *Elyna bellardi* and associates invading *Carex rupestris*-*Sieversia turbinata* dry meadow and converting it to alpine meadow climax, Elynetum.

Climax alpine meadow association; Elynetum.—Accumulation of humus and increased stabilization of the soil layer make conditions less severe for plant development in the dry meadow. A floristic study of this meadow in many places indicates that a larger and larger proportion of the increasing plant cover is furnished by *Elyna bellardi* as mature stages of the meadow develop (Fig. 9). A similar study of mesophytic meadows indicates that with gradual decrease of soil moisture in the habitat, *Elyna* and other species from the dry meadow make up an increasing proportion of the vegetation.

Mesophytic alpine meadow, therefore, comes eventually to be invaded by species with lower moisture requirements. The conflict between the mesophytic vegetation consisting of such species as *Aira caespitosa*, *Poa alpina*, *Festuca brachyphylla*, and *Polygonum bistortoides* on the one hand and *Elyna bellardi* and its associates from the dry meadow on the other is a long

one. Extreme conditions of climate, most decisive probably in periods of little precipitation and high evaporation during the growing season, favor the species of lower water requirement. The mesophytes drop out gradually in more exposed situations, their places being occupied more and more by the xero-mesophytic Elynetum.

The sedge-like *Elyna bellardi* forms an extremely tenacious sod by means of which it appears to be able, once it gains a foothold in this community, to defend itself against dislodgment by its competitors and to spread and dominate the association. Other sod forming species are rare in a well developed climax meadow. And yet, *Elyna* at its best forms a thin ground cover with small openings between the tufted plants. It rarely covers more than 60 to 80% of the surface and frequently occupies less. Viewed from above and close up, the surface of the meadow presents a rough uneven appearance since the tufts of sod project slightly above the surface of the ground. As a result of deposition in the tufts and erosion between them, the depressions between these tufts may reach a depth of 1 to 2 inches. The unevenness is sometimes increased by the dying of old tufts. When viewed from a distance, however, the meadow presents a smooth, even appearance. The stems of *Elyna* may vary in height from 3 to 6 inches, depending on the degree of exposure to wind and sun. Mingled with taller vegetation they may exceed this height. In its general appearance, Elynetum, in contrast with the wet streamside and mesophytic meadows, presents a rather monotonous aspect. While a number of its species have attractive flowers during early summer, the plants are so scattered and in most cases so reduced in stature that they are usually inconspicuous in the meadow. Seasonal change is reduced to a minimum in this *Elyna* dominated association. In late summer and in early spring the dead or faded stems add to the dullness of the landscape.

In the thin stands of the Elynetum, which are more noticeable on exposed slopes, occur a considerable number of members of the dry sedge-Sieversia meadow. In many cases these are considerably reduced in size, are of cushion or rosette form, and spring from a prominent taproot. The plants nestle in the small depressions between the tufts which are so characteristic of the climax meadow. Species appearing quite consistently in such situations are: *Carex rupestris*, *Sieversia turbinata*, *Arenaria sajanensis*, *Selaginella densa*, *Eritrichium argenteum*, *Draba streptocarpa*, *Actinea lanata*, *Lloydia serotina*, *Artemisia scopulorum*, *Luzula spicata*, *Trifolium dasyphyllum*, *Primula angustifolia*, and *Tonestus pygmaeus*. In larger spaces from which they have either never been displaced or in which some destructive agent has made an opening, large polsters and plants of various habits, as well as the preceding species, occasionally appear. Some of these are: *Silene acaulis*, *Paronychia pulvinata*, *Calamagrostis purpurascens*, *Avena mortoniana*, *Festuca brachyphylla*, *Poa rupicola*, *Artemisia pattersoni*, *Ore-*

oxis alpina, *Erigeron pinnatisectus*, *Sedum stenopetalum*, *Campanula uniflora*, and *Rydbergia grandiflora*.

On north slopes and in more mesophytic spots generally throughout this community *Elyna bellardi* does not compete so successfully with other species. Indeed, in such places the leading role may not infrequently be taken by *Sieversia turbinata*. Other species sharing in a conspicuous way in the community under such conditions are: *Polygonum bistortoides*, *P. viviparum*, *Aira caespitosa*, *Festuca brachyphylla*, *Poa pattersoni*, *Oreoxis alpina*, *Trifolium parryi*, and *Sedum integrifolium*. Inability of *Elyna* to dominate these stations may follow because a higher soil moisture content enables mesophytic species to grow more vigorously, while *Elyna* finds optimum conditions at somewhat lower soil moisture where it encounters less competition with mesophytes.

Of primary importance in determining the distribution of *Elyna* and *Sieversia*, in fact of most of the plants of the alpine zone, is the matter of snow cover and length of growing season. Best developed Elynetum occurs on areas where little or no snow accumulates and the growing season is at least ten to twelve weeks long (Figs. 10, 11). *Elyna* appears to be snow avoiding while *Sieversia* develops best where it has winter snow cover and may occur where late lying snow reduces the growing season to six or seven weeks. Even in rather mesophytic locations on north slopes *Elyna* is often prominent and sometimes assumes the leading role in the community where snow melts early. Species occurring in both somewhat mesophytic and in drier, more exposed parts of the climax meadow are: *Carex rupestris*, *Polygonum viviparum*, *Oreoxis alpina*, *Trifolium dasyphyllum*, *Tonestus pygmaeus*, and *Silene acaulis*.

Elynetum may develop at any altitude above timberline but occurs most extensively between 11,000 and 12,000 feet on relatively mature and stable soils of intermediate water relations and moderate exposure. It is not more widespread because so small a proportion of the region has reached the stage of development suited to the climax meadow. Soil reactions in many well developed areas of this community showed a variation from pH 5.4 to 6.0 with best development of the association at about pH 5.6. Table XI summarizes studies made of five stands of climax meadow of different altitudes, exposures, and degrees of slope. These examples emphasize the consistent floristic composition of the association, the relatively large degree of dominance exercised by *Elyna* in spite of its incomplete cover, and the apparent inability of the companion species to offer serious competition to *Elyna*.

The development of a climax association of a xerophytic character in the alpine region with its relatively high precipitation and humidity may be questioned. If due consideration be given to the magnitude of the forces involved and to the severity of the conditions which must always exist at this high altitude, even after the theoretical equilibrium between climate, soil, and



FIG. 10. *Elyna bellardi* dominating large expanse of stable alpine area on James Peak at 12,000 feet. Small depressions show where erosive action of the wind has torn out holes in the soil.



FIG. 11. Elynetum. Detail showing unusually luxuriant development of *Elyna bellardi* in a somewhat mesophytic portion of the alpine meadow climax.

TABLE XI—*Alpine Meadow Climax: Elynetum*

Number of stand.....	1	2	3	4	5
Size of Sample.....	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M	.1 sq. M
Number of samples scored.....	20	40	20	20	20
Altitude.....	11,900	11,300	11,700	13,000	11,800
Exposure.....	S	E	N	SE	SW
Slope.....	5°	8°	20°	8°	10°
Wind influence.....	exposed	exposed	moderate	exposed	exposed
pH of root layer.....	5.6	6.0	5.4	5.4	5.6
Vegetation cover %.....	85	85	90	85	85
<i>Elyna bellardi</i>	5.4	5.3	5.3	5.4	5.3
<i>Carex rupestris</i>	5.1	5.1	5.1	5.1	5.2
<i>Sieversia turbinata</i>	5.1	3.1	5.2	5.1	3.1
<i>Polygonum viviparum</i>	5.1	5.1	5.1	1.1	2.1
<i>Lloydia serotina</i>	5.1	5.1	5.1	4.1	3.1
<i>Selaginella densa</i>	5.1	4.1	1.1	3.1	4.1
<i>Arenaria sajanensis</i>	2.1	5.2	1.1	4.1	3.1
<i>Campanula uniflora</i>	1.1	5.1	3.1	—	4.1
<i>Actinea lanata</i>	1.1	5.1	+	—	+
<i>Eritrichium argenteum</i>	1.1	1.1	+	3.1	1.1
<i>Silene acaulis</i>	1.1	1.1	1.1	4.1	+
<i>Lucula spicata</i>	1.1	1.1	+	1.1	1.1
<i>Oreoxis alpina</i>	+	+	+	+	5.1
<i>Poa rupicola</i>	+	2.1	1.1	+	+
<i>Trifolium dasyphyllum</i>	+	—	2.1	+	2.1
<i>Trifolium nanum</i>	+	+	—	4.1	+
<i>Festuca brachyphylla</i>	+	1.1	+	+	+
<i>Artemisia pattersoni</i>	+	2.1	1.1	—	—
<i>Thalaspi coloradoense</i>	+	+	—	+	+
<i>Saxifraga rhomboidea</i>	+	+	—	+	3.1
<i>Rydbergia grandiflora</i>	+	—	+	+	1.1
<i>Castilleja occidentalis</i>	+	—	+	—	+
<i>Arenaria aequicaulis</i>	—	1.1	+	+	+
<i>Arenaria fendleri</i>	—	1.1	—	+	+
<i>Sedum stenopetalum</i>	—	2.1	—	+	+
<i>Primula angustifolia</i>	+	—	2.1	5.1	—
<i>Potentilla saximontana</i>	+	—	—	+	+
<i>Cerastium beerlingianum</i>	+	—	+	+	—
<i>Draba streptocarpa</i>	—	+	—	+	+
<i>Tonestus pygmaeus</i>	+	—	—	2.1	—
<i>Polygonum bistortoides</i>	—	—	+	—	+
<i>Aira caespitosa</i>	1.1	—	+	—	—
<i>Dryas octopetala</i>	—	+	1.1	—	—
<i>Erigeron pinnatisectus</i>	—	1.1	—	+	—
<i>Erysimum nivale</i>	—	—	—	+	+
<i>Phlox caespitosa</i>	—	—	—	+	1.1
<i>Saxifraga flagellaris</i>	+	—	—	—	+
<i>Trietion spicatum</i>	—	—	+	+	—
<i>Gentiana romanovii</i>	—	—	2.1	+	—
<i>Trifolium parryi</i>	—	—	3.1	—	—
<i>Castilleja brachyantha</i>	—	+	—	—	—
<i>Thalictrum alpinum</i>	—	—	1.1	—	—
<i>Paronychia pulvinata</i>	—	—	—	2.1	—
<i>Allium pikeanum</i>	—	3.1	—	—	—

vegetation shall have been reached, it seems reasonable that rather xeric conditions must always prevail over most of the region and that the only vegetation fitted to succeed would be composed largely of xero-mesophytes. In regard to the soil reaction which will ultimately exist, it appears reasonable to

conclude that since the soil arises from silicate rocks which are deficient in basic materials and since the action of both climate and vegetation tend to increase this acidity, the final product can not be other than acid. In the Swiss Alps where precipitation and humidity are both apparently higher than in the Colorado Rockies and where a permanent snow cap persists to moisten the slopes in the alpine zone, investigation has shown that the ultimate vegetation for most of the region—the *Curvuletum*—is rather xerophytic, and that even in regions with underlying limestone the soil reaction is distinctly acid. As to the importance of the soil reaction in determining the ultimate floristic composition of the climax meadow, the writer is in doubt, but it seems quite possible that indirectly it is a factor of importance in its relation to the maintenance of the rather general impoverished condition of the soil in the dry alpine meadow.

The ability of *Elyna bellardi* by means of its vigorous and extensive root system to assume almost complete control of the soil in its habitat means that competition for water and nutrients in the community is severe. Plants with low demands for these materials and with qualities enabling them to endure the severe exposure of the rather open habitat stand the best chance of succeeding in the meadow with the dominating *Elyna*. Small xerophytic species from fell field and dry meadow communities and moderately mesophytic species from the mesophytic meadow appear best adapted to such conditions. Such plants are most prominent as companion species in the *Elynetum*.

ALPINE SUCCESSION

The course of development of alpine vegetation has already been traced in a detailed manner from its beginning on exposed rocks through different pioneer associations of dry habitats, through dry meadow to the climax meadow; and from its beginning along stream and lake margins through various types of wet meadow and sedge moor to the climax meadow. The diagram in Figure 12 summarizes in a general way the main lines of succession as indicated by the present study.

The xerarch sere begins with species of xerophytic lichens on bare rock surfaces. Less xerophytic foliose lichens succeed these and are followed by xerophytic mosses which form small polsters. The latter sometimes serve as germinating beds for disseminules of certain pioneer humus-requiring plants. Seeds finding lodgment on polsters or in cracks and crevices of rocks germinate, and the seedlings survive for a time. Eventually accumulation of humus and erosion products results in the formation of a poor soil which makes possible the completion by pioneer species of their entire life cycle. Vegetation gradually increases on ledges, among boulders, on fell fields and slides, with resultant progress in soil development. A meadow-like vegetation is developed on stable areas of accumulated soil. This dry meadow of rather impoverished vegetation, characterized through most of its extent

by *Carex rupestris* and *Sieversia turbinata* but occasionally dominated locally for long periods of time on stony slopes by the shrub association of *Dryas octopetala*, is ultimately succeeded by the xero-mesophytic sedge meadow climax vegetation in which the leading role is taken by *Elyna bellardi*.

The hydrarch sere begins in streams and lakes or about wet stony areas or snow drifts. Hydrophytic species of flowering plants form wet meadows

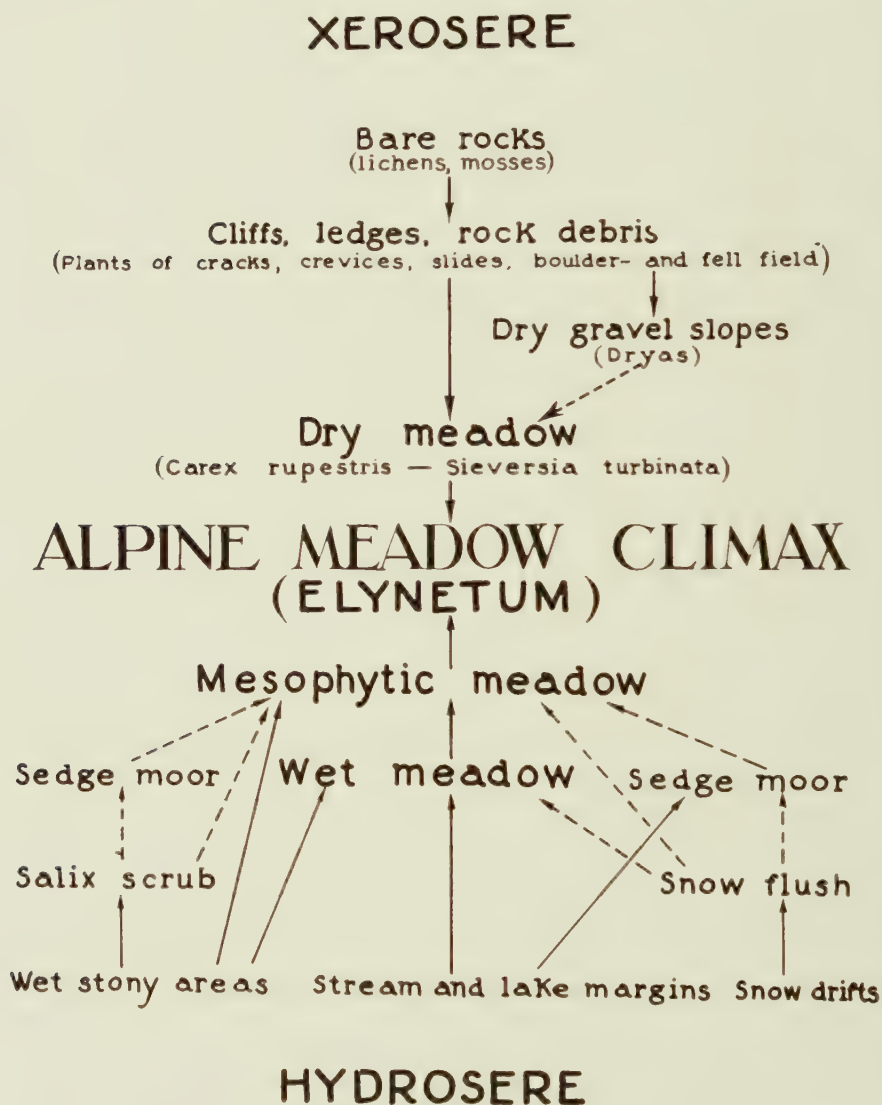


FIG. 12. Diagrammatic representation of the main lines of alpine plant succession in xero- and hydroseres. Especially long enduring locally distributed edaphic associations can be recognized by the broken lines which continue beyond them.

along stream and lake margins, or snow flush meadows where late melting snow saturates the soil during an abbreviated growing period. In places of relatively high and constant water relations sedge moors sometimes develop. Coarse wet gravels are frequently populated by willow communities, or they may also sometimes develop into sedge moors. Decreasing soil water content in any of these communities, as a result either of building up the soil level by accumulations of humus and mineral matter or of more efficient drainage, is followed by invasion by species of lower water requirements. Mesophytic meadow is the result. Still further lowering of the water content in the habitat eventually permits the entrance into the community of *Elyna bellardi* and other xero-mesophytes. These constitute the climax meadow vegetation or Elynetum which appears best suited to succeed itself indefinitely under the extreme climatic conditions of the alpine region.

ALPINE PLANTS OF JAMES PEAK

The first definite information concerning vegetation and climate of alpine altitudes in the Rocky Mountains came from botanical explorations made during the nineteenth century. As early as 1824 Torrey (1824) enumerated new or rare plants from the Rocky Mountains, and a few years later (Torrey 1828) he gave an account of plant collections which had been made by Dr. Edwin P. James during an expedition to the Rocky Mountains in the summer of 1820. Dr. Charles C. Parry (1862, 1868) made several trips into the Colorado Rockies in the decade from 1860 to 1870, collecting and enumerating many species of alpine plants, and describing physiographic and climatic conditions in the high mountain regions. Hall and Harbour accompanied Parry on his western journey in 1862 and collected many plants throughout the region.

Most of the plants brought back from the mountains passed under the careful scrutiny of such men as Torrey, Gray (1863), Englemann, and Parry in this country, and many of them were sent to Hooker and other prominent European authorities. The names of these early botanists are perpetuated alike in the names of the species and of the peaks of these high mountains. Among the names prominent on pages of Rocky Mountain floras of more recent years none appear more frequently perhaps than those of Rydberg and A. Nelson.

As has always happened in the history of the biological sciences, the rather fascinating work of collecting and identifying the species made much more rapid progress than the investigation of ecological and physiological relationships. Discussions concerning probable centers of origin and possible lines of migration of the genera and species constituting the present Rocky Mountain flora, based upon present and past geographical distribution of these and closely related groups in the high mountains and in the arctic regions of both eastern and western hemispheres, are given by Rydberg

(1914) and Holm (1927). Publications by these two botanists give details concerning present distribution and racial affinities, so far as they are known, of many of the species occurring in the vicinity of James Peak.

The alpine vegetation of James Peak shows pronounced northern affinities. Many of the species occur in the far North where the alpine zone descends to the arctic lowland. There they frequently range clear across the continent. The study made by Holm (1927) of the geographic distribution and the floristic affinities of a number of strictly alpine species occurring on the higher Colorado peaks shows that many of the species collected on James Peak during the present investigation are circumpolar, that a considerable number occur in the Alps of central Europe, and some in the high mountains of central Asia. The following are a few of the species which are circumpolar and occur in the Alps: *Silene acaulis*, *Arenaria sajanensis*, *Stellaria longipes*, *Sagina saginoides*, *Oxyria digyna*, *Lloydia serotina*, *Polygonum viviparum*, *Erigeron uniflorus*, and *Luzula spicata*.

In general, circumpolar species which also occur on high mountain ranges far to the south are regarded as having originated in the arctic regions long before the glacial period, at which time they were able to migrate southward to these mountains. Upon the retreat of the ice sheet a number of species of more southern origin probably followed the melting ice and in this way became a part of the arctic flora.

Disjunct species of widely separated regions, if they have a single point of origin, as is generally believed, possibly represent species of a former extensive range which have disappeared from intervening spaces. Their probable centers of origin are usually determined by studying their geographic distribution in connection with the distribution of all closely allied groups.

Endemic species have probably originated in more recent times within their present areas. Some endemic species of common occurrence on James Peak are: *Lychnis montana*, *Claytonia megarrhiza*, *Trifolium nanum*, *Saxifraga chrysantha*, *Oreoxis alpina*, *Eritrichium argenteum*, *Chionophila jamesii*, *Mertensia alpina*, *Synthyris alpina*, and *Primula angustifolia*.

Floristic affinity studies point to four principal centers of origin for the alpine species: (1) the Rocky Mountain alpine, (2) the Arctic, (3) the European alpine, and (4) the Asiatic alpine. A number of species are believed to have moved up into the alpine zone from lower altitudes. Some of these are: *Dasiophora fruticosa*, *Kalmia polifolia*, *Arctostaphylos uva-ursi*, *Vaccinium oreophilum*, *Campanula rotundifolia*, *Pedicularis groenlandica*, and *Aira caespitosa*.

The alpine vegetation on James Peak may therefore be considered as made up of species (1) of Alpine origin consisting (a) of plants originating in the Rocky Mountains since the ice age, and (b) of plants from alpine regions of other continents originating before the ice age; (2) of Arctic origin preceding the ice age; and (3) of lowland origin either before or since the

glacial period. A few species, like *Pinus aristata*, have their main range south of James Peak. The latter is possibly an endemic species originating in the subalpine zone farther south.

The following list of species collected in the vicinity of James Peak includes plants reaching their uppermost limit in the wind timber of the alpine-subalpine transition belt as well as the true alpine species which are common in the region above tree limit. Consequently some of the names are not always included in lists of alpine plants. Species encountered only in the wind timber are indicated by the asterisk (*) and no attempt was made to determine their lower altitudinal limit.

One set of the collections upon which this report is based is deposited in the Herbarium of the Field Museum at Chicago; and one is retained by the writer.

ALPINE PLANTS OF JAMES PEAK

Ophioglossaceae

**Botrychium lanceolatum* (Gmel.) Augs.

Polypodiaceae

Cryptogramma acrostichoides R. Br.

**Polystichum lonchitis* (L.) Roth

Filix fragilis (L.) Gilib.

Lycopodiaceae

Lycopodium selago L.

**Lycopodium annotinum* L.

Selaginellaceae

Selaginella densa Rydb.

Selaginella underwoodii Hieron.

Pinaceae

**Pinus flexilis* James

**Pinus aristata* Engelm.

**Pinus murrayana* Balf.

**Picea engelmanni* (Parry) Engelm.

**Abies lasiocarpa* (Hook) Nutt.

**Juniperus communis sibirica* (Burgsd.) Rydb.

Gramineae

Stipa lettermanni Vasey

Phleum alpinum L.

**Agrostis hiemalis* (Walt) B. S. P.

**Calamagrostis canadensis* (Michx) Beauv.

Calamagrostis purpurascens R. Br.

Aira caespitosa L.

**Aira atropurpurea* Wahl.

Trisetum spicatum (L) Richt.

- Trisetum wolfii* Vasey
Avena mortoniana Scribn.
Danthonia intermedia Vasey
Poa alpina L.
Poa arida Vasey
Poa fendleriana (Steud) Vasey
Poa grayana Vasey
Poa interior Rydb.
Poa pattersoni Vasey
Poa pudica Rydb.
Poa reflexa Vasey and Scribn.
Poa rupicola Nash
Festuca brachyphylla Schult.
Festuca rubra L.
**Bromus ciliatus* L.
Agropyron scribneri Vasey
Agropyron tenerum Vasey

Cyperaceae

- **Eleocharis tenuis* (Willd.) Schultes
Elyna bellardi (All) Degl.
Elyna macrocarpa Clokey ined.
**Carex aquatilis* Wahl.
Carex arapahoensis Clokey
Carex atrata L.
Carex capillaris L.
Carex capitata L.
Carex chalciolepis Holm
Carex ebenea Rydb.
Carex festiva Dewey
Carex festivella Mack.
Carex illota Bail.
Carex misandra R. Br.
Carex nigricans C. A. Meyer
Carex noxa Bail.
Carex nubicola Mack.
Carex petasata Dewey
Carex phaeocephala Piper
Carex pratensis Drej.
Carex pyrenaica Wahl.
**Carex rossii* Boott.
Carex rupestris All.
Carex scopulorum Holm

Carex siccata Dewey

Carex variabilis Bail.

Juncaceae

**Luzula subcapitata* Rydb.

Luzula spicata (L.) DC.

Luzula parviflora (Ehrh.) Desv.

Juncus mertensianus Bong.

Juncus triglumis L.

Juncus castaneus Smith

Juncus parryi Engelm.

Liliaceae

Allium pikeanum Rydb.

Lloydia serotina (L.) Sweet

Melanthaceae

Zygadenus elegans Pursh

Orchidaceae

**Limnorchis stricta* (Lindl.) Rydb.

**Listera nephrophylla* Rydb.

Salicaceae

**Populus tremuloides* Michx.

Salix barclayi Anders.

Salix pseudolapponum von Seemen (*S. glaucops* And. of authors)

Salix petrophila Rydb.

Salix chlorophylla Anders.

Salix saximontana Rydb.

Salix nivalis Hooker

Salix monica Bebb. (*S. planifolia monica* (Bebb) Schn.)

Betulaceae

Betula glandulosa Michx.

Polygonaceae

**Eriogonum subalpinum* Greene

Eriogonum xanthum Small

Oxyria digyna (L.) Camptdera

Polygonum bistortoides Pursh.

Polygonum bistortoides linearifolium (Wats.) Small

Polygonum viviparum L.

**Polygonum aviculare* L.

**Polygonum engelmanni* Greene

Chenopodiaceae

**Chenopodium leptophyllum* (Moq.) Nutt.

**Monolepis nuttalliana* (R. & S.) Engelm.

Portulacaceae

Claytonia megarrhiza (Gray) Parry

Lewisia pygmaea (Gray) Robins

Caryophyllaceae

- Silene acaulis* L.
Lychnis montana Wats.
**Lychnis drummondii* Wats.
Stellaria umbellata Turcz.
Stellaria longipes Goldie
Cerastium beeringianum Cham. & Schlect.
Cerastium arvense L.
Sagina saginoides (L.) Brit.
Arenaria acqicaulis A. Nels.
Arenaria sajancensis Willd.
Arenaria fendleri Gray
Paronychia pulvinata Gray

Ranunculaceae

- Caltha rotundifolia* (Huth) Greene
**Trollius albiflorus* (Gray) Rydb.
**Aquilegia coerulea* James
Aquilegia saximontana Rydb.
**Anemone globosa* Nutt.
**Pulsatilla hirsutissima* (Pursh) Brit.
Ranunculus drummondii Greene
Ranunculus alpeophilus A. Nels.
Ranunculus pedatifidus J. E. Smith
Ranunculus alismacifolius Geyer
Ranunculus adoneus Gray
Thalictrum alpinum L.

Papaveraceae

- Papaver radicum* Roth.

Cruciferae

- Thlaspi coloradoense* Rydb.
Thlaspi glaucum A. Nels.
**Roripa alpina* (Wats.) Rydb.
**Cardamine cordifolia* Gray
**Capsella bursa-pastoris* Medik.
Draba fladnizensis Wulf.
Draba cana Rydb.
Draba crassifolia Grahm.
Draba aurea Vahl.
Draba streptocarpa Gray
Draba chrysantha Wats.
**Arabis drummondii* Gray
**Arabis divaricarpa* A. Nels.
Erysimum nivale (Greene) Rydb.

Crassulaceae

- Sedum stenopetalum* Pursh
- Sedum integrifolium* (Raf.) A. Nels.
- Sedum rhodanthum* Gray

Saxifragaceae

- **Parnassia fimbriata* Banks, Kon. & Sims
- Heuchera parvifolia* Nutt.
- Heuchera bracteata* (Torr.) Ser.
- **Mitella pentandra* Hook.
- Saxifraga flagellaris* Willd.
- Saxifraga chrysantha* Gray
- Saxifraga debilis* Engelm.
- Saxifraga cernua* L.
- Saxifraga austromontana* Wiegand.
- Saxifraga caespitosa* L.
- **Saxifraga arguta* Don.
- Saxifraga rhomboidea* Greene
- **Saxifraga austrina* A. Nels.

Grossulariaceae

- **Ribes montigenum* McClatchie
- **Ribes coloradoense* Coville
- **Ribes lacustre* (Pers.) Poir

Rosaceae

- Dryas octopetala* L.
- **Rubus strigosus* Michx. (*R. melanopsis* Focke)
- Dasiophora fruticosa* (L.) Rydb.
- Sibbaldia procumbens* L.
- **Fragaria ovalis* (Lehm.) Rydb.
- Potentilla crinita* Gray
- Potentilla nelsoniana* Rydb.
- Potentilla quinquefolia* Rydb.
- Potentilla nivea* L.
- Potentilla uniflora* Ledeb.
- Potentilla glaucophylla* Lehm.
- Potentilla saximontana* Rydb.
- Potentilla diversifolia* Lehm.
- Sieversia turbinata* (Rydb.) Greene

Leguminosae

- Trifolium nanum* Torr.
- Trifolium parryi* Gray
- Trifolium dasyphyllum* T. & G.

Violaceae

- Viola biflora* L.

Viola bellidifolia Greene

**Viola blanda* Willd.

Onagraceae

Chamaenerion latifolium L.

Chamaenerion angustifolium (L.) Scop.

Epilobium lactiflorum Haussk.

Umbelliferae

Oreoxis alpina (Gray) C. & R.

**Angelica grayi* C. & R.

Pseudocymopterus montanus (Gray) C. & R.

Pyrolaceae

**Pyrola secunda* L.

**Pyrola minor* L.

**Moneses uniflora* (L.) Gray

Ericaceae

**Kalmia polifolia* Wang.

**Gaultheria humifusa* (Graham) Rydb.

**Arctostaphylos uva-ursi* (L.) Spreng.

Vacciniaceae

Vaccinium oreophilum Rydb.

**Vaccinium caespitosum* Michx.

Primulaceae

Primula angustifolia Torr.

Primula parryi Gray

Androsace subumbellata A. Nels.

Gentianaceae

Chondrophylla americana (Engelm.) A. Nels.

Gentiana monantha A. Nels.

**Gentiana plebeja* Cham.

Gentiana plebeja holmii Wettst.

Gentiana romanzovii Ledeb.

**Gentiana parryi* Engelm.

Swertia palustris A. Nels.

Swertia congesta A. Nels.

Frasera speciosa Griseb.

Polemoniaceae

Phlox caespitosa var. *condensata* (Gray) E. Nels.

**Polemonium pulcherrimum* Hook.

Polemonium confertum Gray

Hydrophyllaceae

Phacelia sericea (Graham) Gray

Boraginaceae

**Lappula* sp.

Eritrichium argenteum Wight.

Mertensia alpina (Torr.) Don

Mertensia bakeri lateriflora (Greene) A. Nels.

Mertensia ovata Rydb.

Mertensia ciliata (Torr.) Don

Scrophulariaceae

**Penstemon glaucus stenosepalus* Gray

**Penstemon alpinus* Torr.

Chionophila jamesii Benth.

Synthyris alpina Gray

Veronica alpina L.

**Veronica serpyllifolia* L.

**Pedicularis racemosa* Dougl.

Pedicularis grayi A. Nels.

Pedicularis parryi Gray

Pedicularis scopulorum Gray

Pedicularis groenlandica Retz.

Castilleja brachyantha Rydb.

Castilleja occidentalis Torr.

**Castilleja lauta* A. Nels.

Castilleja rhexifolia Rydb.

Caprifoliaceae

**Sambucus microbotrys* Rydb.

Adoxaceae

**Adoxa moschatellina* L.

Campanulaceae

Campanula uniflora L.

Campanula rotundifolia L.

Valerianaceae

**Valeriana edulis* Nutt.

Valeriana acutiloba Rydb.

Compositae

**Chrysopsis pumila* Greene

Tonestus pygmaeus (T. & G.) A. Nels.

Tonestus lyallii (Gray) A. Nels.

Solidago decumbens Greene

**Aster apricus* (Gray) Rydb.

Aster culminus A. Nels.

Machaeranthera pattersonii (Gray) Greene

Erigeron salsuginosus Gray

Erigeron salsuginosus var. *glacialis* (Nutt.) Gray

**Erigeron elatior* (Gray) Greene

**Erigeron superbus* Greene

- Erigeron melanocephalus* A. Nels.
Erigeron uniflorus L.
**Erigeron leiomeris* Gray
Erigeron debilis (Gray) Rydb.
**Erigeron compositus* Pursh
**Erigeron compositus discoideus* Gray
Antennaria parvifolia Nutt.
**Antennaria rosea* (Eat.) Greene
Antennaria concinna A. Nels.
Antennaria aprica Greene
**Antennaria pulcherrima* (Hook.) Greene
**Anaphalis subalpina* (Gray) Rydb.
Chaenactis alpina (Gray) Jones
Actinea lanata (Nutt.) Kuntze
Rydbergia grandiflora (Pursh) Greene
Achillea subalpina Greene
Artemisia borealis Pall.
Artemisia scopulorum Gray
Artemisia pattersonii Gray
Artemisia saxicola Rydb.
**Arnica cordifolia* Hook.
**Arnica pumila* Rydb.
**Arnica ventorum* Greene
**Arnica subplumosa* Greene
**Arnica rydbergii* Greene
**Arnica parryi* A. Gray
**Senecio kuntzei* Rydb.
**Senecio purshianus* Nutt.
**Senecio amplexans* A. Gray
Senecio holmii Greene
Senecio taraxacoides (Gray) Greene
Senecio carthamoides Greene
**Senecio triangularis* Hook.
**Senecio crassulus* Gray
Senecio atratus Greene
**Senecio werneriaefolius* Gray
Senecio petrocallis Greene
**Senecio fendleri* Gray
Senecio crocatus Rydb.
Carduus sp.
Crepis sp.
Hieracium gracile Hook.
**Agoseris glauca* (Nutt.) Greene

**Agoseris aurantiaca* (Hook.) Greene

**Agoseris purpurea* (Gray) Greene

Taraxacum scopulorum (Gray) Rydb.

**Taraxacum mexicanum* DC.

Taraxacum ceratophorum (Ledeb.) DC.

DISCUSSION

Regions of moderate altitude and latitude usually lie well within limits of temperature and growing season critical for species constituting their vegetation. Consequently these factors are of minor importance in determining the species present. Soil moisture frequently assumes first place in such locations, and other environmental factors rank about in accord with their effect upon soil moisture relations. Under conditions of moderate rainfall and low humidity which obtain during summer on the prairie, Weaver (1931) finds soil moisture and humidity most important in controlling floristic composition.

On the vegetation frontier in the alpine zone both rainfall and humidity are relatively high. Here, where growing season and temperature are near their limit for plant life, these factors assume first rank in determining the species which constitute the vegetation. In a region of such rigid conditions for plant life it seems probable that any factor having much effect upon the environment may prove at times to be limiting for the existence of particular species. Regardless of how favorable other environmental conditions may be, the short growing season limits decidedly the number of species which can persist at this high altitude. No such sweeping statement may be made in regard to temperature. Many species can tolerate even lower temperatures than occur in any part of the alpine zone. Still, temperature does set the upper limit for a number of alpine plants, though less frequently perhaps than does the brief growing season. Due to persistence of snow drifts or to low light intensity the growing period is so short that certain places support no vegetation at all, and on large areas the best vegetation possible is very meager.

It must not be thought, however, that soil moisture is unimportant in alpine habitats. A consideration of conditions existing in various plant communities furnishes convincing evidence to the contrary. In the distribution within these communities of the species which are able to complete their life cycles during the few weeks of growing weather, in spite of frosts which may occur at any time, the water relations existing in the various habitats appear more often than any other single factor to be controlling. This fact is brought out in a prominent way in the study of alpine plant succession.

In regard to factors important in the distribution of species at high altitudes it might be said in general that temperature and length of growing

season are of primary importance in controlling the vertical distribution while soil moisture is probably first in determining the horizontal distribution into various habitats at any given level. Of course the term "level" is used in a broad sense, as length of growing season and temperature rarely, if ever, vary consistently with altitude. The longest persisting snow drifts frequently lie well down in the alpine zone. Cold air flows down and late frosts frequently occur in narrow valleys or ravines far below the mountain summits. It has already been noted that late frosts and short growing season, in combination with the desiccating effect of winds at times when soil water is deficient, are important in fixing the upper limit of tree species below that of herbaceous plants. To a somewhat more limited degree these same factors working together set the upper limits of many herbaceous species. A considerable number of herbaceous plants, however, may be found growing at any altitude in the alpine zone restricted of course to their particular habitat. Soil moisture relations more often than any other condition impose this restriction. In other words, temperature and growing season sometimes become of minor consideration in the distribution of alpine species.

The strong wind affects the water relations within the plant by decreasing soil water as a result of accelerated evaporation rate and by increasing transpiration rate. Dead branches and deformed trees of wind timber, patches of dead vegetation on windswept slopes, and strict zonation of species according to degree of wind exposure constitute evidence of the important role of wind in determining the alpine species and their distribution. Erosion, distribution of soil, pollination, and seed dispersal are other important activities performed by wind.

Precipitation and humidity are both relatively high, but both undergo considerable fluctuation during the growing season. During periods with little rainfall, strong wind, and bright sunlight, humidity and soil water are both reduced at a time when the evaporation rate is high. Only in stream or lake margin communities or in mesic habitats where exposure is less severe can plants of high water requirements survive. Even in such places the water supply may be reduced temporarily, and soil moisture may sink below the limit necessary for survival of certain species.

Snow is of value as a protection during winter for certain species as well as for its conserving effect upon the moisture supply for the summer. On the other hand, there are the snow avoiding species which occur only where snow does not accumulate. Wind is quite important in connection with the disposition of snow cover. While light has an important influence both in relation to photosynthetic activity and in its effect upon evaporation rate, it appears that the majority of the species have light requirements well within the extreme limits of light intensity of the region.

Alpine soils are in general rather consistently nutrient-poor, acid in reaction, and immature in development. Most alpine species appear to have a

considerable range of soil tolerance. The most immediate effect arising from differences in the amount of humus present in various habitats is probably the resulting difference in water holding capacity of the soil.

It seems, therefore, that in the distribution of alpine species throughout the region, length of growing season, temperature, and soil moisture relations probably play the leading role; wind, evaporation, precipitation, humidity, light, and soil, except in extreme cases, are to be regarded as of secondary importance. Furthermore the dwarfed condition of the vegetation appears to result from the brief growing period and from deficient water relations within the plant due to frequent low soil temperatures and occasional rainless periods with high evaporation rates. Intense light and poor soil contribute to this stunted condition. In exposed positions high wind affects the growth mechanically as well as physically. Biotic factors, with the exception of forest fires, which have sometimes brought about the downward extension of alpine conditions and vegetation beyond the former alpine-subalpine border, appear to have had little influence upon the vegetation.

In tracing the course of development of alpine vegetation it appears that in both hydrosere and xerosere, so long as one deals with areas in which the growing season is sufficient for progressive development by the vegetation, the primary influence in bringing about the successional development is changing conditions in soil moisture. These changes in habitat are necessarily accompanied by changes in the floristic composition of the plant community. Associations appear, develop to maturity, and gradually give way to new ones, probably more in response to changing water relations in the habitat than to other conditions although other factors must constantly be considered. Floristic studies made in the same type of community at different altitude and exposure show some differences, of course, in species present; but in general there is considerable uniformity in the dominants and the characteristic species.

The lines of development as indicated by floristic changes point to a gradual convergence towards a fairly uniform meadow vegetation which appears where the soil becomes fairly well developed and as nearly stabilized by vegetation as the severe climate and strong relief of the region will permit. The vegetation has reached this climax stage of development on broad gentle slopes and on small isolated areas in the more stable situations. The characteristic species of the climax association, the Elynetum, must be more or less xerophytic in order to succeed under the rather rigid conditions for plant development which prevail on the high mountain slopes.

Parts of the region, where the vegetation is prevented by long-enduring local conditions in the soil from progressing noticeably towards the climax stage for extremely long periods of time and where characteristic and distinctive plant communities persist, support edaphic climax types or associations. Ultimately these areas too appear to yield to the combined in-

fluence of climate and vegetation and are invaded by the species from the climax meadow.

SUMMARY

1. Environmental conditions and vegetation were studied in the alpine zone on James Peak during the growing seasons of 1928 and 1929.

2. Alpine climate approaches that of the arctic in severity. The growing season varies from three to twelve weeks. The daily temperature range during summer is excessive. The days are moderate to warm, but frost may occur almost any night. Growing season, temperature, and soil moisture are of first importance in determining species present, their distribution, and the dwarfed condition of the plants.

3. Light intensity is high and is connected with the reduced size of plants and modified leaf structure. Light accelerates evaporation and affects the distribution of species.

4. The total precipitation and the humidity are relatively high but undergo considerable fluctuation during the growing season. Most of the precipitation occurs in the form of snow during the resting period of the plants. Snow serves as winter protection for certain species and conserves some of the winter precipitation for use during the summer. Run off is high.

5. Strong winds are characteristic of alpine climate. Wind influences the disposition of winter snow, accelerates evaporation, reduces soil moisture content, and exerts a very pronounced effect upon the vegetation as shown by wind timber and fell field communities.

6. Daily evaporation rates become excessive during rainless periods in summer when humidity is low. Conditions at such times are critical for vegetation.

7. Biotic factors have probably had little influence upon the vegetation.

8. Alpine vegetation consists of scrub forest, grassland, and desert.

9. Alpine scrub occupies the alpine-subalpine transition zone and consists of deformed tree species which offer protection to communities of intermingling alpine and subalpine plants.

10. Alpine desert includes sparsely populated communities of pioneer species of the rocks, of slides, and of areas where late-lying snow or low light intensity permit the development of little or no vegetation. Fell field and boulder field communities in advanced stages represent the best developed vegetation of the alpine desert. Dicotyledonous herbs dominate and constitute the principal members of these pioneer communities.

11. Alpine grassland constitutes the larger portion of the vegetation of the alpine zone and includes several rather distinct types of alpine meadow which owe their differences in floristic composition primarily to differences in soil moisture relations. Scrub associations dominated by *Dryas* on exposed

stony slopes and by species of *Salix* on wet gravels frequently interrupt the continuity of the alpine meadow.

12. In the development of the vegetation cycle the xerosere begins on the rocks. Lichen-moss associations of bare rock surfaces are succeeded by pioneer communities of cracks, crevices, and accumulated rock waste. Dry meadows, or sometimes scrub associations, develop and are eventually followed by the climax sedge meadow, *Elynetum*.

13. The hydrosere begins along stream and lake margins where wet meadows or sometimes moor communities composed of hydrophytes develop. Gradual and progressive decrease in soil moisture content eventually leads to invasion of these communities by species of lower moisture requirements. Mesophytic and ultimately climax meadow, *Elynetum*, follow.

14. Long enduring conditions at any of these stages may result in fairly well defined edaphic climax associations.

15. Most of the alpine species range far to the north of Colorado. A considerable number occur in the arctic where they are circumpolar. Some species found on James Peak occur on the high mountains of central Europe and Asia.

16. The alpine flora consists of endemic species which have probably originated in the Rocky Mountains, of disjunct species, some of which have probably originated in the arctic and some in high mountains of Europe or Asia, and of species concerning which the center of origin is doubtful since they have a continuous range over alpine and arctic regions in both eastern and western hemispheres.

BIBLIOGRAPHY

- Blackwelder, E. and H. H. Barrows. 1911. *Elements of Geology*. New York. 1-475. 485 fig.
- Braun-Blanquet, J. 1932. *Plant Sociology*. The study of plant communities. Translated, revised, and edited by George D. Fuller and Henry S. Conard. New York. xviii + 439. 180 fig.
- Braun-Blanquet, J. et J. Pavillard. 1925. *Vocabulaire de sociologie vegetale*. Montpellier. 1-22.
- Braun-Blanquet, J. und H. Jenny. 1926. *Vegetations-Entwicklung und Bodenbildung in der alpinen Stufe der Zentralalpen*. Herausgeg. Kom. S. N. G. Erforsch. Nat.-Parks, Denkschr. Schweiz. Naturf. Gesells. 63 (2): 183-349.
- Brockmann-Jerosch, H. 1919. *Baumgrenze und Klimacharakter*. Beiträge zur geobotanischen Landesaufnahme. 6: 1-255. Zürich.
- Cain, S. A. and R. C. Friesner. 1929. Some ecological factors in secondary succession: Upland hardwood, I. Evaporation studies in the Sycamore Creek region. Butler Univ. Bot. Studies 1: 1-15.
- Dodds, G. S. 1917. Altitudinal distribution of Entomostraca in Colorado. Proc. U. S. Nat. Mus. 54: 59-87.
- Fries, T. C. E. 1913. *Botanische Untersuchungen in nordlichsten Schweden*. Upsala und Stockholm. viii + 361. 99 fig.

- Fuller, G. D. 1914. Evaporation and soil moisture in relation to the succession of plant associations. *Bot. Gaz.* **58**: 193-234.
- George, R. D. 1927. Geology and natural resources of Colorado. Univ. of Colo. Semicentennial Publications 1877-1927. Boulder, Colo. xv + 228.
- Gray, Asa. 1863. Enumeration of the species of plants collected by Dr. C. C. Parry and Messrs. Elihu Hall and J. P. Harbour during the summer and autumn of 1862 on and near the Rocky Mountains in Colorado Territory, lat. 39°-41°. Philadelphia Acad. Nat. Sci. Proc. (1863): 55-80.
- Heer, Oswald. 1836. Die Vegetationsverhältnisse des südöstlichen Teils des Kantons Glarus, Mitt. aus dem Gebiete der theoretischen Erdkunde. Herausgeg. v. J. Fröbel und O. Heer. I. Zürich.
- Henrici, M. 1918-19. Chlorophyllgehalt und Kohlensäureassimilation bei Alpen- und Ebenenpflanzen. *Verhandl. Naturforsch. Gesells. Basel* **30**.
- Holm, Theo. 1927. The vegetation of the alpine region of the Rocky Mts. in Colorado. *Nat. Acad. Sci. Mem.* 19, **3**: 1-45.
- Parry, C. C. 1862. Physiographical sketch of that portion of the Rocky Mountain range, at the headwaters of South Clear Creek, and east of Middle Park: With an enumeration of the plants collected in this district in the summer months of 1861. *Amer. Jour. Sci. & Arts.* 2nd. Ser. **33**: 231-243; 404-411.
1868. On the character of the persistent snow accumulations in the Rocky Mountains, lat. 40°-41° north, and certain features pertaining to the alpine flora. *Trans. St. Louis Acad. Sci.* **2**: 532-543.
- Ramaley, F. 1917. Soil moisture index. *Bot. Gaz.* **63**: 151-152.
1919. The role of sedges in some Colorado plant communities. *Amer. Jour. Bot.* **6**: 120-130.
1920. Subalpine lake shore vegetation in north-central Colorado. *Amer. Jour. Bot.* **7**: 57-74.
- Raunkiaer, C. 1918. Recherches statistiques sur les formations vegetal. *Det. Kgl. Danske Videns. Selskab. Biol. Meddel.* I, **3**: 1-80.
- Rydberg, P. A. 1914. Phytogeographical notes on the Rocky Mountain region: II. Origin of the alpine flora. *Bull. Torr. Bot. Club.* **41**: 89-103.
- Schanz, F. 1918. Einfluss des Lichtes auf die Gestaltung der Vegetation. *Ber. deutsch Bot. Gesells.* **39**: 619-632.
1918. Wirkung des Lichtes auf die Pflanze. *Biol. Zentralbl.* **38**: 283-296.
1919. Wirkung des Lichtes verschiedener Wellenlänge auf die Pflanzen. *Ber. deutsch Bot. Gesells.* **37**: 430-442.
- Schimper, A. F. W. 1903. *Plant Geography*. Oxford. xxx + 839.
- Shaw, C. H. 1909. The causes of timberline on mountains: the role of snow. *Plant World* **12**: 169-181.
- Torrey, J. 1824. Descriptions of new or rare plants from the Rocky Mountains, collected in July, 1820 by Dr. Edwin James. *N. Y. Ann. Lyc. Nat. Hist.* **1**: 30-36.
1828. Some account of a collection of plants made during a journey to the Rocky Mountains in the summer of 1820 by Edwin P. James, M. D., Asst. Surgeon U. S. Army. *N. Y. Ann. Lyc. Nat. Hist.* **2**: 161-254.
- Warming, E. 1909. *Oecology of plants*. Oxford. xi + 422.
- Weaver, J. E. 1914. Evaporation and plant associations in southeastern Washington and adjacent Idaho. *Plant World* **17**: 273-294.
- Weaver, J. E. and F. E. Clements. 1929. *Plant Ecology*. New York. xx + 520. 262 fig.
- Weaver, J. E. and W. J. Himmel. 1931. The environment of the prairie. *Univ. Neb. Conserv. and Surv. Div. Bull.* **5**: 1-50.
- Whitfield, C. J. 1933. The ecology of the vegetation of the Pike's Peak region. *Ecol. Monog.* **3**: 75-105.

